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FIELD OBSERVATIONS ON THE BEET LEAFHOPPER, EUTETTIX TENELLUS, IN CALIFORNIA[1]

HENRY H. P. SEVERIN[2]

(Contribution from the Division of Entomology and Parasitology, California Agricultural Experiment Station, cooperating with the United States Department of Agriculture, Bureau of Entomology.)

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[1] Received for publication May 18, 1932.

[2] Associate Entomologist in the Experiment Station.

INTRODUCTION

During 1918–1932 field investigations were carried on to determine where the beet leafhopper spends the winter and to locate the natural breeding areas in this state. Trips were taken to Death Valley, Mojave Desert, Imperial Valley, and the Tulare Lake and Bakersfield sections of the San Joaquin Valley—areas from which Ball[2] believed the beet leafhopper migrated into sugar-beet fields—and also to the middle and northern sections of the San Joaquin Valley, to the Sacramento Valley, Santa Clara, and Salinas valleys, and to all other important sugar-beet districts in California. After a general survey of this enormous territory, it soon became evident that it would require many years of field work to map the natural breeding areas of this insect, and hence the work was limited to the San Joaquin, Sacramento, Santa Clara, and Salinas valleys and to several small valleys. No foothill investigation has been carried on in Death Valley, Antelope Valley, Mojave Desert, and Imperial Valley. Such results as were obtained in these districts have been published in previous papers. [28, 30, 40]

The host plants of the beet leafhopper on the uncultivated plains and foothills, in the cultivated areas, and the original native host plants, the spring and summer dispersals and migrations, natural barriers, causes of fluctuation in population, and natural enemies were also observed during the investigations.

DISTRIBUTION OF BEET LEAFHOPPER

The beet leafhopper is a native species and has been taken in western North America from Canada into Mexico. Davis[11] found the northern limit of the leafhopper was Cache Creek, British Columbia, 140 miles north of the international boundary. Carter[10] used the climograph as a means of comparing climates with respect to precipitation and temperatures in determining the probable limits of the range of the beet leafhopper; these studies were supplemented with surveys of the distribution of the insect. He considers that the presence of the leafhopper in British Columbia is due to a northward migration. Carter[9] published the results of the Canadian survey conducted by H. L. Seamans and states that the leafhopper was not found in the province of Alberta, although the results of the survey were not conclusive. Davis[11] found that the leafhopper was generally distributed in western Washington and Oregon. The area west of the Cascade Mountains in Oregon and

Washington represents the high-rainfall belt of the Pacific Northwest and is a limiting factor of the breeding range of the pest, although migrations into these areas occur.[10] Henderson[7] found that the beet leafhopper occurred in Lower California and western Mexico as far south as Guasave, Sinola. The insect was not found on the high central plateau, which extends from the southern portion of Durango to Mexico City.

BREEDING AREAS

If nymphs of the spring generation are found year after year in a region, then that region can be considered as a permanent natural breeding area; on the other hand, when these nymphs are found only during a favorable year, that locality should be considered as a temporary breeding district. This leafhopper migrates long distances, and when insects migrate from their natural breeding grounds they fail to establish themselves in their new environment unless they meet conditions similar to their original habitat. In California the presence of pale-green adults of the spring generation, the pale-yellow forms of the summer generation, or the dark overwintering adults of the autumn generation, is no indication of a natural breeding area of the beet leafhopper. To map the natural breeding areas and migratory regions in some of the valleys in California required many years of field investigations.

In San Joaquin Valley.—The Great Interior Valley of California occupies the central part of the state. The valley is almost 400 miles long and from 20 to 50 miles wide and extends in a general northwest-southeast direction. It is bounded on its eastern side by the lower foothills of the Sierra Nevada Mountains and on its western side by the Inner Coast Range. The valley is enclosed around its northern end by the Klamath Mountains and around its southern end by the Tehachapi Mountains. The northern third of the Great Basin forms the Sacramento Valley and the remainder, the San Joaquin Valley. The San Joaquin and Sacramento valleys are not separated by a mountain barrier. The Marysville Buttes are located near the middle part of the Sacramento Valley, a few miles northwest of Marysville.

The northern limit of the breeding range of the beet leafhopper in the San Joaquin Valley was found to be in a canyon in the Inner Coast Range situated about 4 miles southwest of Pittsburg (fig. 1). The natural breeding area includes the canyons of the Inner Coast Range in the northern San Joaquin, the plains and foothills of the middle and southern San Joaquin, and the foothills of the Tehachapi Mountains.

The plains and foothills of most of Kern County are natural breeding grounds except the Sierra Nevada foothills near the northern end of the county. The northern limit of the breeding range on the Sierra Nevada foothills was found to be about 10 miles north of Porterville near Lindsay in Round Valley (fig. 1). The natural breeding area extends into the mountain passes of the Inner Coast Range for a distance of 12 miles in Little Panoche, Big Panoche, and Cholame passes.

In Panoche Valley.—A natural breeding area occurs between the Coast Ranges on the western foothills of the Panoche hills bounding Panoche Valley. When the hills are covered with shrubs and trees, as is

Fig. 1. Relief map of California showing natural breeding areas of beet leafhopper on plains and foothills in the San Joaquin Valley indicated by black dots. The northern third of the Great Basin represents the Sacramento Valley, which is a migratory area of the beet leafhopper.

the case on the Outer Coast Range, beet leafhoppers are rarely captured on red-stem filaree (*Erodium cicutarium*) (fig. 2), the most important breeding plant on the plains and foothills in California.

In Salinas Valley.—The Salinas Valley is the largest of the many valleys inclosed within the Coast Ranges in California. From Monterey Bay it extends in a southeasterly direction, in a line parallel with the

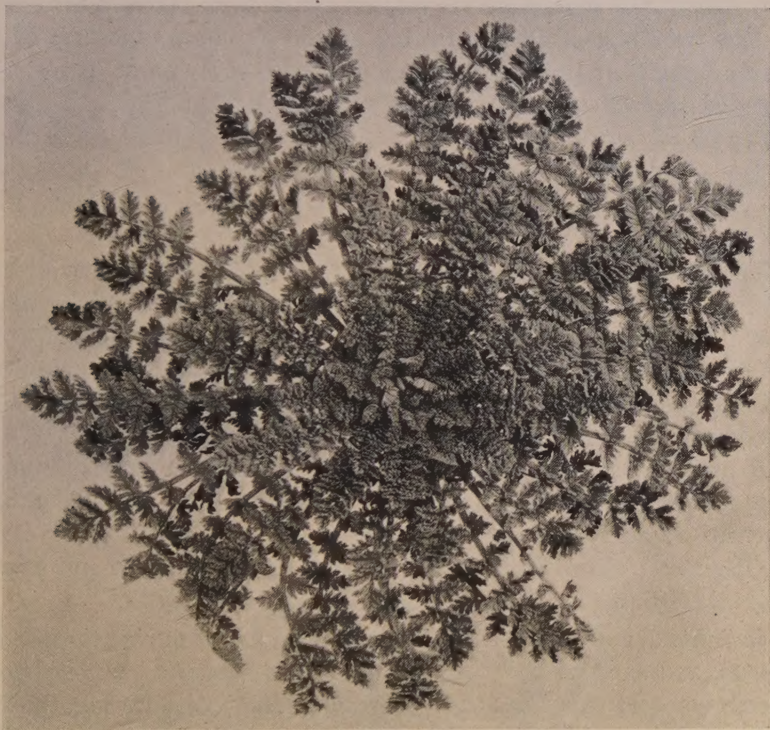

Fig. 2. Rosette form of red-stem filaree (*Erodium cicutarium*), which is the most important food and breeding plant on the plains and foothills, of the beet leafhopper in California.

coast, to its head, a few miles southeast of Santa Margarita—a distance of about 100 miles. Its average width is from 7 to 9 miles. Upon the northwest the valley is bounded by Monterey Bay; upon its sides by the Sierra Santa Lucia and Sierra Salinas ranges, with their outlying spurs upon the west; and by the Gabilan Mountains and Inner Coast Range upon the east, the latter separating the Salinas Valley from the San Joaquin Valley of the interior of the state.

The northern limit of the foothill breeding range on the Gabilan Mountains in the Salinas Valley is near the boundary of the fog belt south of Soledad, and the southern limit is in the vicinity of San Miguel,

the most favorable foothill breeding area extending from Greenfield to Bradley. During the autumn adults have been taken on the foothills of the Sierra Santa Lucia Mountains bounding the coastal side of the Salinas Valley and nymphs have been taken on the foothills about 5 miles southwest of King City, but this mountain range is only a minor natural breeding area.

In Santa Ana Valley.—Nymphs and adults were taken in the spring of 1926 on red-stem filaree growing on the southern exposures of the barren foothills in the Santa Ana Valley, south of Hollister. The eastern foothills were forested and no leafhoppers were taken.

In Panoche and Pacheco Passes.—During the spring of 1925 and 1926 a high population of nymphs and adults was found on the foothills in the vicinity of Paicines and in the western entrance of Panoche Pass, but no nymphs were taken in Pacheco Pass.

Suttie[3] found on November 24, 1931, from 10 to 15 overwintering adults to 100 sweeps of the insect net on perennials and red-stem filaree near Paicines and south toward the entrance of Panoche Pass. He also found on November 8, 1930, as many as 20 to 30 overwintering adults to 100 sweeps of the insect net on perennials growing along the San Benito River near Hollister.

A natural breeding area of the beet leafhopper extends from the Santa Ana Valley to Panoche Pass, becoming less favorable toward Pacheco Pass. In all probability the origin of the leafhopper in the Hollister beet district was from this natural breeding area and in some years through migrations from the San Joaquin Valley.

In Santa Clara Valley.—Investigations conducted during the autumn, winter, and spring of 1925–26 demonstrated that the beet leafhopper breeds on short red-stem filaree growing in rocky localities on the foothills extending out into the valley from two Coast Ranges in the southern part of the Santa Clara Valley. An occasional nymph and adult of the spring generation were taken on red-stem filaree in rocky localities on the foothills east of Coyote. This is a minor and temporary natural breeding area.

Suttie collected on January 11, 1927, an occasional overwintering adult on red-stem filaree in rocky localities on the foothills near Lick and Coyote.

In Sierra Nevada Valleys.—Natural breeding areas of the beet leafhopper occur in valleys located in the Sierra Nevada. Nymphs and adults were found on red-stem filaree growing sparingly on the rocky

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[3] W. Suttie, of the Spreckels Sugar Company, in a personal interview with the author.

hillsides surrounding the southwestern portion of Honey Lake Valley (altitude 4,000 feet). Overwintering adults were taken in Sierra Valley (altitude 5,000 feet) during 1925, and adults of the spring generation were found in this valley by Hartung during 1919 and Schwing during 1924, as reported in a previous paper.[32] The leafhopper and curly top of sugar beets were also reported in the same paper as occurring in Indian Valley (altitude 3,600 feet) and American Valley (altitude 3,400 feet).

Fig. 3. Branch of arrowscale (*Atriplex phyllostegia*), showing leaves and fruiting bracts, also characteristic leaves and fruiting bracts removed from plant.

HOST PLANTS

On Uncultivated Plains and Foothills

Food Plants.—There existed on the plains and foothills of California an abundance of grasses, clovers, and wild flowers, until man disturbed the native conditions. As early as 1773, the Spaniards disturbed the native conditions by introducing sheep which carried in their wool seeds of plants from the Mediterranean Basin. The ensuing competition between the native and introduced plants greatly diminished most of the native species.

Red-stem filaree, which occurs on the barren hillsides and dry plains has been considered an introduced species, but there is some difference of opinion among botanists. If this plant was introduced, then a special adaptation of the leafhopper to it has occurred.

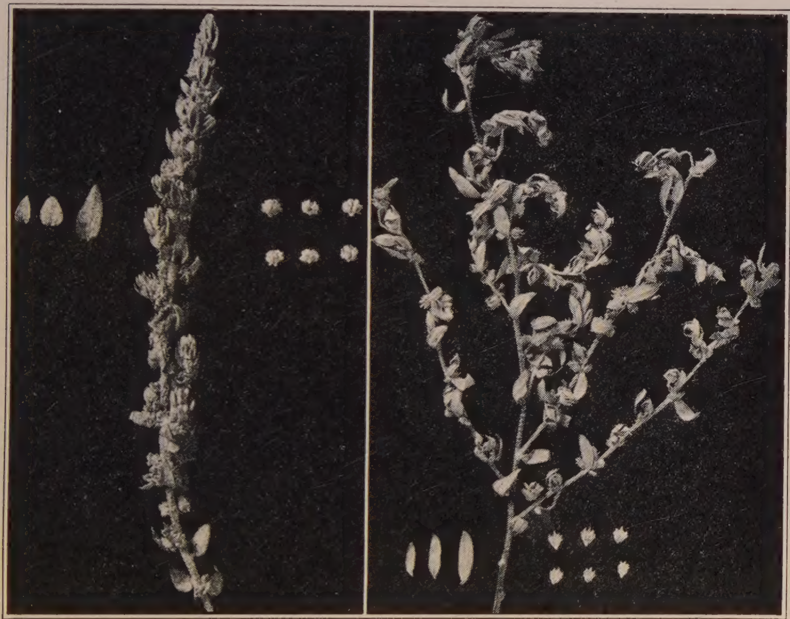
Cattle and sheep have overgrazed the preferred introduced forage plants, so that these were not permitted to produce seeds abundantly. It is these overgrazed foothills sparsely covered with red-stem filaree in the semiarid regions that are the most favorable habitat of this insect.

Fig. 4. Twigs of fleshscale or Australian saltbush (*Atriplex semibaccata*), showing leaves and fruiting bracts, also different-shaped leaves and fruiting bracts removed from plant. This perennial saltbush was introduced into California about thirty years ago from Australia as a forage plant, and is one of the most important food and breeding plants of the beet leafhopper in the Imperial Valley. It is also a favorable host plant of the leafhopper in the San Joaquin and Salinas valleys, but is not abundant in the Sacramento Valley. It is well established in the southern part of the state and is common in the fog belt.

The disturbance of the native conditions on the plains and foothills and in the cultivated areas increased the most favorable food and breeding plants of the leafhopper and hence has increased the opportunities for an enormous multiplication of the pest when climatic conditions are favorable.

The relative numbers of beet leafhoppers captured on plants growing on the plains and foothills of the Coast Range bounding the San Joaquin Valley were determined during 1918. The insects were taken on twenty species of plants, five of which belong to the saltbush family. The reader is referred to a previous paper[28] for a list of food plants.

Breeding Plants.—The beet leafhopper has been bred from five different species of annual plants growing on the foothills of the San Joaquin Valley: red-stem filaree (*Erodium cicutarium*) and white-stem filaree or musk filaree (*E. moschatum*) (Geraniaceae), *Hollisteria lanata* (Polygonaceae), *Malvastrum exile* (Malvaceae), and common peppergrass (*Lepidium nitidum*) (Cruciferae). Red-stem filaree is the most impor-



A *B*

Fig. 5. *A*, Branch of crownscale (*Atriplex coronata*), showing leaves and fruiting bracts, also leaves and fruiting bracts removed from plants. *B*, Branch of ballscale (*Atriplex fruiticulosa*), showing leaves and fruiting bracts, also leaves and fruiting bracts removed from plant. During dry autumns before the pasture vegetation has germinated, beet leafhoppers are commonly taken on this plant on the plains of the San Joaquin Valley.

tant host plant upon which the overwintering adults feed and deposit their eggs, and upon which the spring generation develops.

The nymphs hatched from eggs deposited in the leaves or stems of the following perennial Chenopodiaceae growing on the plains of the San Joaquin Valley: ballscale (*Atriplex fruticulosa*), spinescale (*A. spinifera*), and Australian saltbush or fleshscale (*A. semibaccata*).

In Cultivated Areas

Food Plants.—The relative numbers of beet leafhoppers captured on plants growing in the cultivated areas of the San Joaquin Valley were determined in 1918. The insects were taken on thirty species of

plants,[28] eighteen of which belong to the Chenopodiaceae. After the invasion of the cultivated areas by the pest, the leafhoppers were more abundant on plants of the family Chenopodiaceae, to which the sugar beet belongs.

During the spring the beet leafhopper was found in enormous numbers on short-lived annual saltbushes, such as arrowscale (*Atriplex*

A *B*

Fig. 6. *A*, Branch of silverscale or fogweed (*Atriplex argentea expansa*), showing leaves and fruiting bracts. *B*, Branch of redscale or red orache (*Atriplex rosea*), showing leaves and fruiting bracts, also fruiting bracts removed from plant.

phyllostegia) (fig. 3; plate 1, *B*); heartscale (*A. cordulata*) (plate 1, *F*; plate 3, *C*); crownscale (*A. coronata*) (fig. 5 *A*; plate 1, *E*); brittlescale (*A. parishi*) (plate 1, *I*; plate 3, *A*); but during the summer when these saltbushes become dry except in irrigated fields, the leafhoppers assemble on other favorable host plants. It was frequently noticed that when the stems of other species of plants became woody the insects left, but this was not the case with fogweed or silverscale (*A. argentea expansa*) (fig. 6*A*; plate 1, *A*); red orache or redscale (*A. rosea*) (fig. 6*B*; plate 1, *C*); bractscale (*A. bracteosa*) (plate 1, *D*; plate 3, *D*); and Russian

Fig. 7. Vacant field covered with bractscale (*Atriplex bracteosa*).

Fig. 8. Bractscale (*Atriplex bracteosa*) growing along a fence, showing height of plant, which may vary from 1 to 15 feet, and with stems commonly spreading to form dense tangled mats from 1 to 10 feet across, from which arise slender erect or ascending twigs.

This annual saltbush forms dense communities in the San Joaquin Valley, and owing to its size and abundance, is one of the most important food and breeding plants of the beet leafhopper in the cultivated areas of California. The leafhoppers are commonly found on this weed from the time that the spring dispersal from the plains and foothills begins until the return flights occur.

thistle (*Salsola kali tenuifolia*). The leafhoppers remained on these plants until the leaves became dry.

Wherever man has disturbed the native conditions in the San Joaquin Valley, vast areas of annual saltbushes occur. Saltbushes grow abundantly along fences (fig. 8), roadsides, highways (fig. 9), and railroad tracks (fig. 10), on vacant fields (fig. 7), and, after the grain is harvested, on stubble fields, and commonly around hay and straw stacks. Dense masses surround alkali sinks (fig. 11), although the black alkali is often too strong for their development. Irrigation and drainage

Fig. 9. Bractscale (*Atriplex bracteosa*), growing along highway.

Fig. 10. Silverscale or fogweed (*Atriplex argentea expansa*), growing along railroad tracks.

canals are favorable locations for the development of this alkali vegetation (fig. 13).

The stimulus for the development of enormous areas of annual saltbushes in the San Joaquin Valley has probably been the increase of alkali lands by man's activities. According to Kelly[23] "several hundred thousand acres in the San Joaquin Valley, which were comparatively free from alkali previous to the advent of irrigation, have already been seriously injured, or abandoned." He states that alkali finds its way into good lands by the use of saline irrigation water, and by the rise of the ground-water level through seepage and overirrigation.

Fig. 11. Alkali sink surrounded by dense growths of redscale or red orache (*Atriplex rosea*).

Fig. 12. Plains of the western San Joaquin Valley covered with spinescale (*Atriplex spinifera*), a perennial saltbush, which serves as a food plant of the beet leafhopper during dry autumns and winters before the pasture vegetation has germinated.

Breeding Plants.—The most important factor in the enormous increase of the beet leafhopper in the San Joaquin Valley is the abundance of the breeding plants in the cultivated areas. The plants upon which enormous numbers of nymphs and adults were taken in the field are representatives of the Chenopodiaceae. The leafhopper was bred from eggs deposited under natural conditions in thirty-eight species of weeds growing in the cultivated regions. The weeds upon which adults were collected were removed with the root system from vacant fields, stubble

Fig. 13. Bractscale (*Atriplex bracteosa*), growing along an irrigation canal.

fields, beet fields, truck-crop fields, along roadsides, railroad tracks, rivers, and irrigation and drainage canals. Table 1 lists the plants in which the beet leafhopper deposited eggs in the cultivated districts and shows which are native to this country and which introduced from other countries.

Later investigations have shown that the nymphs are not able to acquire the winged stage by feeding on some of the weeds in which eggs are deposited. The breeding experiments indicate that the most favorable host plants in the cultivated areas are plants of the Chenopodiaceae, to which the sugar beet belongs.

The host plants of the beet leafhopper among economic plants was reported in previous papers.[34, 37]

TABLE 1

LIST OF WEEDS IN WHICH BEET LEAFHOPPERS DEPOSITED EGGS IN CULTIVATED AREAS UNDER NATURAL CONDITIONS IN CALIFORNIA*

Common name	Scientific name	Family	Origin	Valley in which breeding plants were obtained
		Annual saltbushes		
Arrowscale	*Atriplex phyllostegia* Wats.	Chenopodiaceae	Native	San Joaquin
Bractscale	*Atriplex bracteosa* Wats.	Chenopodiaceae	Native	San Joaquin, Sacramento, Salinas
Brittlescale	*Atriplex parishi* Wats.	Chenopodiaceae	Native	San Joaquin, Sacramento
Crownscale	*Atriplex coronata* Wats.	Chenopodiaceae	Native	San Joaquin, Sacramento
Fogweed (silverscale)	*Atriplex argentea expansa* (Wats.)	Chenopodiaceae	Native	San Joaquin, Sacramento, Salinas
Heartscale	*Atriplex cordulata* Jepson	Chenopodiaceae	Native	San Joaquin, Sacramento
Spear orache (spearscale)	*Atriplex patula* L.	Chenopodiaceae	Native	Sacramento
....	*Atriplex tularensis* Coville	Chenopodiaceae	Native	San Joaquin
Wheelscale	*Atriplex elegans* (Moq.) Dietr.	Chenopodiaceae	Native	Imperial
Red orache (redscale)	*Atriplex rosea* L.	Chenopodiaceae	Introduced	San Joaquin, Sacramento, Salinas
		Perennial saltbushes		
Australian saltbush (fleshscale)	*Atriplex semibaccata* R. Br.	Chenopodiaceae	Introduced	San Joaquin, Sacramento, Salinas, Imperial
		Pigweeds		
....	*Chenopodium leptophyllum* Wats.	Chenopodiaceae	Native	San Joaquin
Lamb's quarters (white pigweed)	*Chenopodium album* L.	Chenopodiaceae	Introduced	San Joaquin, Sacramento, Salinas
Sowbane (nettleleaf goosefoot)	*Chenopodium murale* L.	Chenopodiaceae	Introduced	San Joaquin, Sacramento
Mexican tea	*Chenopodium ambrosioides* L.	Chenopodiaceae	Introduced	San Joaquin, Sacramento
		Other weeds		
....	*Nitrophila occidentalis* (Moq.) Wats.	Chenopodiaceae	Native	San Joaquin, Sacramento
Russian thistle	*Salsola kali* L. var. *tenuifolia* G. F. W. Mey.	Chenopodiaceae	Introduced	San Joaquin, Sacramento, Salinas
(*Continued*)				

* The saltbushes were determined by H. M. Hall, Carnegie Institution of Washington, and all other weeds were classified by various systematists of the Division of Botany, University of California.

TABLE 1—(*Concluded*)

Common name	Scientific name	Family	Origin	Valley in which breeding plants were obtained
	Other Weeds—(*Continued*)			
... .	*Suaeda depressa* (Pursh) var. *erecta* Wats.	Chenopodiaceae	Native	San Joaquin
Curly dock	*Rumex crispus* L.	Polygonaceae	Introduced	San Joaquin, Sacramento, Salinas
Wire grass (yard grass)	*Polygonium aviculare* L.	Polygonaceae	Introduced	San Joaquin
Rough pigweed	*Amaranthus retroflexus* L.	Amaranthaceae	Introduced	San Joaquin, Sacramento, Salinas
Tumbleweed	*Amaranthus graecizans* L.	Amaranthaceae	Introduced	San Joaquin, Salinas
....	*Amaranthus deflexus* L.	Amaranthaceae	Introduced	San Joaquin, Salinas
Indian chickweed	*Mollugo verticillata* L.	Aizoaceae	Native	San Joaquin
Lowland purslane	*Sesuvium sessile* Pers.	Aizoaceae	Native	San Joaquin, Imperial
Red maids	*Calandrina caulescens* H. B. K. var. *menziesii* Gray	Portulacaceae	Native	San Joaquin
Common purslane	*Portulaca oleracea* L.	Portulacaceae	Introduced	San Joaquin
Charlock	*Brassica arvensis* (L.) B. S. P.	Cruciferae	Introduced	San Joaquin, Sacramento
Wild radish	*Raphanus sativius* L.	Cruciferae	Introduced	Salinas
Jackass clover	*Wislizenia refracta* Engelm.	Cruciferae	Native	San Joaquin
Spanish clover	*Lotus americanus* (Nutt.) Bisch.	Leguminosae	Introduced	San Joaquin
Dwarf mallow	*Malva rotundifolia* L.	Malvaceae	Introduced	Salinas
Cheese weed	*Malva parviflora* L.	Malvaceae	Introduced	San Joaquin
Alkali mallow	*Sida hederacea* (Dougl.) Torr.	Malvaceae	Native	San Joaquin
Orchard morning-glory	*Convolvulus arvensis* L.	Convolvulaceae	Introduced	Sacramento
Chinese pusley	*Heliotropium curassavicum* L.	Boraginaceae	Native	San Joaquin, Salinas
Horehound	*Marrubium vulgare* L.	Labiatae	Introduced	Salinas
Tolguacha (jimson weed)	*Datura meteloides* D. C.	Solanaceae	Native	San Joaquin, Salinas
... ..	*Solanum douglasii* Dunal.	Solanaceae	Native	Salinas
Horseweed	*Erigeron canadensis* L.	Compositae	Native	San Joaquin
Cotton-batting plant	*Gnaphalium chilense* Spreng.	Compositae	Native	Sacramento
Common sunflower	*Helianthus annuus* L.	Compositae	Native	San Joaquin
Common spikeweed	*Centromadia pungens* (T. & G.) Greene	Compositae	Native	San Joaquin
Spiny clotbur	*Xanthium spinosum* L.	Compositae	Introduced	San Joaquin, Salinas
Mayweed	*Anthemis cotula* L.	Compositae	Introduced	San Joaquin

Original Native Host Plants

The distribution of insects is often limited by the geographical range of native food and breeding plants. The most important host plants of the beet leafhopper are representatives of the Chenopodiaceae (saltbush family) and Cruciferae (mustard family). H. M. Hall has prepared a brief statement concerning the geographical distribution of the species of saltbushes as follows: "There are numerous species of atriplexes (saltbushes) throughout western North America as far south as tropical Mexico, the number of species as well as individuals diminishing toward the south."

Perennials.—As shown in table 2, *Atriplex nuttalli* and *A. nuttalli falcata* are the only perennial saltbushes which serve as breeding plants of the beet leafhopper in states other than California; all others are food plants.

The beet leafhopper occurs abundantly on certain perennial saltbushes in the San Joaquin Valley during dry autumns. There are on the plains of the western San Joaquin Valley vast areas of shrubby perennial saltbushes (fig. 12). A comparison of the natural breeding grounds of the leafhopper with the distribution of the perennial saltbushes in valleys where an intensive study of both has been made follows.

Cattle spinach or allscale (*Atriplex polycarpa*) (fig. 14*A*; plate 2, *B*) is one of the most favorable shrubby perennial saltbushes as a food plant of the leafhopper. According to W. C. Cook it was found in Los Banos Creek, 10 miles southwest of Los Banos in the middle San Joaquin Valley, and extends as far south as the Tehachapi Mountains. This saltbush is green during dry autumns. Lower populations of leafhoppers are obtained when *A. polycarpa* was swept during the afternoon than after sunset. In one test two persons swept these shrubs with an insect net for one hour from 2:40 to 3:40 P.M. and 24 specimens were taken. The same saltbushes were swept for half an hour from 5:15 to 5:45 P.M. and 126 specimens were taken. In all probability the leafhoppers remain within the shrubs during the daytime, and come to the outer branches and foliage at sunset.

Spinescale (*Atriplex spinifera*) (fig. 12; plate 2, *A*) which is sometimes mixed with *A. polycarpa*, is often too dry for large populations of the leafhopper in October, but during November it develops fresh leaves and is a favorable food plant. *A. spinifera* occurs as far north as Volta in the San Joaquin Valley and has been recorded as far south as Buena Vista hills in Kern County. During the 1919 outbreak of the beet leaf-

TABLE 2

PLANTS AMONG THE CHENOPODIACEAE AND CRUCIFERAE USED AS FOOD OR BREEDING PLANTS BY THE BEET LEAFHOPPER

State	Authority	Common name	Scientific name	Origin
		Chenopodiaceae, perennial saltbushes		
Idaho	Haegele[15]	Shadscale	*Atriplex confertifolia* (Torr. & Frem.) Wats.	Native
		Moundscale	*Atriplex muttalli* Wats.	Native
Utah	Knowlton [24,25]		*Atriplex pabularis* Nels.	Native
		Wingscale	*Atriplex canescens* (Pursh) Nutt	Native
		Shadscale	*Atriplex confertifolia* (Torr. & Frem.) Wats.	Native
		Quailbrush, lenscale	*Atriplex lentiformis* (Torr.) Wats.	Native
		Moundscale	*Atriplex nuttalli* Wats.*	Native
		Moundscale	*Atriplex nuttalli falcata* (Jones)*	Native
		Cattle spinach, allscale	*Atriplex polycarpa* (Torr.) Wats.	Native
California	Severin[28,29,30]	Wingscale	*Atriplex canescens* (Pursh) Nutt.	Native
		Ballscale	*Atriplex fruticulosa* Jepson*	Native
		Quailbrush, lenscale	*Atriplex lentiformis* (Torr.) Wats.	Native
		Cattle spinach, allscale	*Atriplex polycarpa* (Torr.) Wats.	Native
		Australian saltbush	*Atriplex semibaccata* Brown*	Introduced
		Spinescale	*Atriplex spinifera* McBr.*	Native
		Chenopodiaceae, annual saltbushes		
Washington	Ball[2]	....	*Atriplex* sp. (?)	Native
Oregon	Ball[2]	....	*Atriplex* sp. (?)	Native
Idaho	Haegele[15]	Red orache, redscale	*Atriplex rosea* L.*	Introduced
	Carter[10]	Red orache, redscale	*Atriplex rosea* L.*	Introduced
Utah	Knowlton[24,25]	Silverscale	*Atriplex argentea* Nutt.*	Native
		Gardenscale, garden orache	*Atriplex hortensis* L.	Introduced(?)
		Spearscale, spear orache	*Atriplex patula hastata* (L.)	Native
		Ribscale	*Atriplex powelli* Wats.	Native
		Red orache, redscale	*Atriplex rosea* L.*	Introduced
		Wedgescale	*Atriplex truncata* (Torr.) Gray*	Native
Isla Raza, Santa Inez Island	Van Duzee[45]	....	*Atriplex* sp. (?)	....
		....	*Atriplex* sp. (?)	....
		Cruciferae		
Idaho	Haegele[15]	Wormseed mustard	*Erysium cheiranthoides* L.	Introduced
		Tumbling mustard	*Norta altissimia* (L.) Britt.*	Introduced
		Green tansy mustard	*Sophia filipes* (Gray) Heller*	Native
		Penny cress, fanweed	*Thlaspi arvensis* L.	Introduced

(Continued)

* Breeding plants; all others are food plants.

TABLE 2—(*Concluded*)

State	Authority	Common name	Scientific name	Origin
		Crucifereae—(*Concluded*)		
Idaho	Carter[10]	Flixweed, herb-sophia	*Sophia sophia* (L.) Britt.*	Introduced
		....	*Sophia filipes* (Gray) Heller*	Native
		Jim Hill mustard	*Norta altissima* (L.) Britt.*	Introduced
		Black mustard	*Brassica nigra* (L.) Koch	Introduced
		Shepherd's purse	*Bursa bursa-pastoris* (L.) Britt.	Introduced
		False flax	*Camelina microcarpa* Andrezej	Introduced
		Blister cress	*Cheirinia repanda* (L.) Link*	Introduced
		Blister cress	*Cheirinia cheiranthoides* (L.) Link	Introduced
		Blister cress	*Cheirinia aspera* (Nutt.) Rydb.	Native
		Malcolmia	*Malcolmia africana* (L.) R. Br.*	Introduced
		Pepper grass	*Lepidium perfoliatum* L.	Introduced
		Pepper grass	*Lepidium pubicarpum* A. Nels.	Native
		Pepper grass	*Lepidium ramosum* A. Nels.	Native
		Pepper grass	*Lepidium densiflorum* Schrad.*	Native
		Tumble mustard	*Norta altissima* (L.) Britt.*	Introduced
		Whitlow grass	*Draba micrantha* Nutt.	Native
Utah	Knowlton[24,25]	Whitlow grass	*Draba nemorosa* L.	Native
		Whitlow grass	*Draba cunefolia* Nutt.	Native
		Water cress	*Sisymbrium nasturtium-aquaticum* L.	Introduced
		Schoenocrambe	*Schoencrambe linifolia* (Nutt.) Greene	Native
		Charlock	*Sinapsis arvensis* L.	Introduced
		Tansy mustard	*Sophia sonne* (Rob.) Greene	Native
		Tansy mustard	*Sophia filipes* (A. Gray) Heller*	Native
		Tansy mustard	*Sophia pinnata* (Walt.) Howell*	Native
		Tansy mustard	*Sophia hartwegiana* (Fourn.) Greene	Native
		Tansy mustard	*Sophia incisa* (Engelm.) Greene	Native
		Tansy mustard	*Sophia longipidicellata* (Fourn.) Howell	Native
		Tansy mustard	*Sophia procera* Greene	Native
		Tansy mustard, flixweed	*Sophia sophia* (L.) Britt.*	Introduced
			Sophia parviflora (Lam.) Standl.*	Introduced

* Breeding plants; all others are food plants.

hopper, nymphs hatched from eggs deposited in the leaves of this perennial saltbush under natural conditions.

Quailbrush or lenscale (*Atriplex lentiformis*) (fig. 14 *B*; plate 2, *C*) is not as favorable a food plant as the previous two species. *A. lentiformis* is more tolerant to alkali and occurs on alkaline flats and river benches and according to Hall and Clements[16] is the next stage in the succession with *A. polycarpa* and *A. spinifera*. *A. lentiformis* occurs as far north as Firebaugh and south to the Tehachapi Mountains.

In the Sacramento Valley no shrubby perennial saltbushes were found. Ballscale (*Atriplex fruticulosa*) (fig. 5*B*; plate 2, *E*), a small

perennial, occurs in the Sacramento Valley from Glenn County south in the San Joaquin Valley. It occurs on both the plains and foothills in the San Joaquin Valley, and leafhoppers are commonly taken on it during dry autumns.

Australian saltbush or fleshscale (*Atriplex semibaccata*) (fig. 4; plate 2, *D*) is common along roadsides, irrigation canals, and fallow fields,

A *B*

Fig. 14. *A*, Cattle spinach or allscale (*Atriplex polycarpa*), showing end of branch with leaves and fruiting bracts. *B*, Quailbrush or lenscale (*Atriplex lentiformis*), showing end of branch with leaves and fruiting bracts, also fruiting bracts removed from plant.

but is not abundant on the uncultivated plains. The leafhoppers are frequently abundant on it during dry autumns. In some years its foliage was destroyed by heavy frosts, but in a warm winter high percentage of males were taken on several acres of it near Wasco as follows: December 10, 1918, 75 per cent and February 16, 1919, 82 per cent. During the 1925 outbreak of the beet leafhopper large numbers of nymphs and adults were found during the summer on *A. semibaccata* growing on the hillsides of the Gabilan Mountains near Metz in the Salinas Valley. The leafhopper was abundant on it during the winter in the Imperial Valley.

The only native shrubby perennial saltbush in the Salinas Valley is *Atriplex lentiformis*, which is not a favorable food plant of the beet leafhopper. It is found in rare patches from Metz south in the valley.

In the natural breeding area of the Santa Ana Valley to the western entrance of Panoche Pass no native perennial saltbushes were found.

The limited distribution of *Atriplex lentiformis* in the Salinas Valley and the absence of native perennial saltbushes in the Santa Ana Valley indicates that the perennial saltbushes were probably not the original native host plants, but simply serve as food plants during dry autumns in California. It could be argued, however, that the beet leafhopper extended its range to the Santa Ana and Salinas valleys, through migrations from the San Joaquin Valley, after the red-stem filaree spread to the foothills.

During the autumn dispersal, leafhoppers are commonly taken on other shrubby perennials growing on the plains and foothills in the San Joaquin Valley, such as *Gutierrezia californica* and *Isocoma veneta,* which are 1 to 2 feet high. Creek senecio (*Senecio douglasii*), which grows to a height of 2 to 6 feet, is another food plant of the overwintering adults during dry autumns, but it is limited in its distribution. It does not form distinct communities and occurs on gravelly plains and dry stream beds in the foothills of the San Joaquin Valley and sandy floor of the Salinas River and its tributaries. In the Salinas Valley the leafhoppers are common on *Lepidospartum squamatum,* a rigid broom-like shrub from 3 to 6 feet high growing in the stream bed of the Salinas River and its tributaries. *L. squamatum* often forms dense stands in canyons and in some of the mountain passes in the San Joaquin Valley, and owing to its wide distribution is one of the most important food plants of the beet leafhopper during dry autumns. There are many other perennials on which the overwintering adults are taken during dry autumns in the San Joaquin and Salinas valleys, and when the insects are abundant they are taken on all green vegetation.

Mortality on Perennials.—A change in food plants from favorable annuals in the cultivated areas to perennials on the plains and foothills may result in a high mortality of the overwintering adults during the autumn dispersal. No experiments have been conducted up to the present time on the longevity of the overwintering adults on different species of perennials. The longevity of the last living male and female beet leafhopper was reported in previous papers[33, 34, 37] on the host range of curly top. It was frequently found that nymphs which hatched from eggs deposited in host plants would acquire the winged stage on food plants that were unfavorable to the adults.

The overwintering adults have well-developed fat bodies and the food requirements are probably not as important as the water requirements during the early autumn. Carter[8] has been able to sustain the life of the insect on tap water for long periods.

Annuals.—Surveys have been made of the host plants of the beet leafhopper in a number of states, and a discussion of the most important host plants in Canada and the United States follows.

Davis[11] collected the beet leafhopper on Russian thistle and mangels in British Columbia and western Washington, and on these same plants and beets in western Oregon.

In Idaho Haegele[15] found that the principal and most widespread host plants of the Chenopodiaceae were *Atriplex rosea*, Russian thistle (*Salsola pestifer*), and *Bassia hirsuta*. Tumbling mustard (*Norta altissima*) and green tansy mustard (*Sophia filipes*) of the Cruciferae were also important hosts of the beet leafhopper during the spring.

Carter[10] found a sequence of host plants of the beet leafhopper throughout the season in central-southern Idaho including three species of mustards (*Sophia sophia, Sophia filipes,* and *Norta altissima*), *Atriplex rosea,* and *Salsola pestifer,* together with occasional hosts such as *Solanum triflorum*. *Salsola pestifer* is the most important late summer and fall host.

Knowlton[25] considers that the most important spring host plants in northern Utah breeding grounds are the following species of Cruciferae: *Cherinia repanda, Norta altissima, Sophia sophia,* and *Lepidium perfoliatum;* and also *Erodium cicutarium,* a representative of the family Geraniaceae. The two most important summer host plants are *Salsola pestifer* and *Atriplex rosea*. The spring host plants listed above again become important fall hosts, carrying the beet leafhoppers until cold weather puts an end to activity.

The most important breeding plant among the annual saltbushes in states other than California is *Atriplex rosea*, an introduced species. It is only the native host plants that can be considered as the original host plants of the beet leafhopper. Among the important California annual saltbushes on which the summer and autumn generations of beet leafhopper develop are *Atriplex argentea expansa, A. bracteosa, A. patula,* and *A. rosea*. The latter becomes dry too early in the fall to maintain large populations of the autumn generation. *Atriplex phyllostegia, A. parishi, A. coronata, A. cordulata,* and *A. elegans* (plate 1, fig. *H*) are short-lived annual saltbushes which usually become dry in July and on which the summer generation of the beet leafhopper develops.

Among the Cruciferae, green tansy mustard (*Sophia filipes* or, according to Jepson[22] *Sisymbrium incisum* var. *filipes*) is a native species on which the beet leafhopper breeds abundantly in Idaho and Utah, but this species (or variety) does not occur in California. In Utah Knowlton[25] has captured nymphs on tansy mustard (*Sophia pinnata*), a native species, but it has not been shown to be a breeding plant of the beet leafhopper in California. Nymphs have been taken on the native pepper grass (*Lepidium densiflorum*) in Utah, but this species does not occur in California. In California nymphs were bred from eggs deposited in common pepper grass (*Lepidium nitidum*) collected in Little Panoche Pass. This species is common on the California plains, low hills, and in the valleys, and extends north to Washington. Further breeding experiments are necessary to determine whether the native mustards were the original host plants on which the spring generation developed.

Davis[11] failed to take the beet leafhopper on red-stem filaree in British Columbia, western Washington, and western Oregon, but his collections were made from August 10 to September 15, 1926, when this plant would probably not serve as a host plant of the insect. According to Haegele,[15] the beet leafhopper was not found on red-stem filaree, which is comparatively rare in Idaho. In northern Utah Knowlton[25] found, as a rule, low populations of the beet leafhopper on red-stem filaree during the spring, but in a few instances high populations were encountered on this plant during the autumn.

It has been generally considered by botanists that red-stem filaree was introduced from the Mediterranean Basin by the Spaniards into Mexico and South America perhaps as early as the sixteenth century, and a little later into California. This plant belongs to the geranium family (Geraniaceae), which is by no means closely related to the saltbush family (Chenopodiaceae). The possibility that the beet leafhopper was accidentally introduced in red-stem filaree from Europe is entirely out of consideration, for, if this plant was introduced into America from the Mediterranean Basin, it was almost certainly through the seeds carried in the wool of sheep.

Two botanists, however, express a different opinion as to the native home of red-stem filaree. According to Brewer and Watson,[5] *Erodium cicutarium* is "very common throughout the state, extending to British Columbia, New Mexico, and Mexico, also widely distributed in South America and the Eastern Continent. It has been generally considered as an introduced species, but is more decidedly and widely at home throughout the interior than any other introduced plant, and according

to much testimony it was as common throughout California early in the present century as now."

Hendry and Kelly[21] found in adobe bricks the seeds or portions of plants of 32 different weeds, 11 of which were recognized by botanists as introduced European species. In the construction of the adobe bricks weeds of all kinds were used as a binder, particularly those with fibrous stems, including filaree. Red-stem filaree (*Erodium cicutarium*) was found in various adobe structures of missions constructed between 1797 and 1834 in various localities of California. They state: "The mere finding of these plants does not prove that they were introduced by the missions, but when the same weed occurs repeatedly in widely separated localities, and when it is remembered that many of these weeds characteristically follow in the wake of cultivation, it would seem that the missions must have played an important part in their dissemination, if not in their actual introduction."

If red-stem filaree was introduced into California, then in all probability the original native host plants, on which the overwintering adults fed and deposited their eggs and on which the spring generation developed, have been greatly reduced in numbers on the plains and foothills through competition with red-stem filaree and other introduced pasture vegetation. The original native host plants of the beet leafhopper on the plains and foothills in California remain unknown up to the present time. However, to assume that the leafhopper changed its egg-laying habits from the perennial shrubby saltbushes to red-stem filaree in California does not seem plausible. As already stated, the perennial saltbushes were probably not the original host plants on which the spring generation developed but simply serve as food plants of the autumn generation during dry autumns.

According to Carter[10] the perennial plants were the principal hosts of the insect before the advent of the now widely scattered introductions, and through natural balance the predominance of the beet leafhopper was prevented.

DISPERSAL AND MIGRATION

Such terms as "dispersal," and "migration" have in the past been used loosely and interchangeably by entomologists. Tutt[43] has pointed to the advisability of discriminating "between those movements which are made by insects from one part of their ordinary breeding grounds to another and those which make sudden and sweeping changes of location far outside of their natural breeding grounds." He has used "dis-

persal'' for the former, and ''migration'' for the latter.[4] When insects migrate outside of their natural breeding areas, the migrants or their offspring are exterminated by unfavorable climatic conditions.

Accordingly, in this paper, *dispersal* of the beet leafhopper has been used for spring and autumn flights within the natural breeding areas, not resulting in extermination of the insect. Spring dispersals are the flights from the uncultivated plains and foothills into the cultivated areas, and the autumn dispersals are return flights from the cultivated areas to the uncultivated plains and foothills in California. *Migration* of the beet leafhopper has been used for flights outside of the natural breeding areas, resulting in the death of the offspring of the migrants.

Ball[(2)] suggests that the flights of the beet leafhopper ''are in the nature of migration, northward in the spring and southward in the fall.'' There is no evidence to show that a return, autumn, southward migration from the migratory regions to the natural breeding areas occurs with the beet leafhopper in California.

Spring Dispersal in San Joaquin Valley

Local Flights in Foothills.—In years when the pasture vegetation did not dry too rapidly, an enormous congregation of spring-generation adults occurred near the San Joaquin entrance of Little Panoche Pass. At sunset the insects became active, flew higher than during the daytime and often came to rest on one's clothes or on the automobile, and the peculiar sexual behavior occurred as described in a previous paper.[(29)] The flights of the leafhoppers farther up the pass were toward the entrance, corresponding to the direction of the wind at sunset. There were years in which more rain fell near the summit than near the entrance of the pass and no congregations occurred toward the mouth of the pass. The adults were then found to be more abundant toward the summit (fig. 15). The leafhoppers prefer gravelly or rocky slopes in Little Panoche Pass, but when the pasture vegetation dries too rapidly in such localities they fly to green vegetation. It appears that the

[4] This use of the word ''migration'' differs from its use with birds, fishes, and certain other animals, where it is restricted to regular movements that constitute a racial custom with a hereditary basis and include a return journey either by the migrants or their offspring. (See, for example, the definition given by Thompson.[(42)]) Such movements rarely, if ever, occur with insects. Tutt,[(43)] who has assembled the facts bearing on the migration and dispersal of insects that have been recorded in the entomological literature during the last century or more, states: ''As a matter of fact, it has never yet been thoroughly shown that the progeny of any [insect] immigrants, which have settled in new quarters, have returned to the home of their ancestors, although it has been considered highly probable in the case of certain locusts, and suggested also in the case of one butterfly, *Anosia archippus.*''

struggle for favorable food is the stimulus which causes the insects to fly from one locality to another in this mountain pass.

Into Cultivated Areas.—The observations on the spring dispersal of the beet leafhoppers from the uncultivated plains and foothills into the cultivated areas of the San Joaquin Valley were made during the 1919 and 1925 outbreaks of the pest, and in years when the population was not at the maximum in numbers. Large flights from the foothills into the cultivated districts usually occur during warm, sultry, calm evenings. During the spring of 1919, three immense swarms of pale-green leafhoppers flew from the uncultivated plains and foothills into the cultivated regions of the San Joaquin Valley; one in the upper or southern part of the valley on April 8, another in the middle portion on April 14, and the third in the northern or lower section on April 28. It is not to be assumed that all of the leafhoppers acquired the winged stage and flew into the cultivated districts on the dates mentioned. In the middle part of the valley, nymphs and adults were still abundant on green patches of pasture vegetation on April 28. No nymphs were captured on dried pasture vegetation on May 14, and the adults were scarce on perennial plants. It is evident that later flights occurred, but after the invasion of the first large swarm into the cultivated regions, it is difficult to determine further movements from the plains and foothills, owing to flights which occur from unfavorable to favorable food plants within the cultivated regions.

During the summer an occasional adult was taken on various plants growing on the plains and foothills and in mountain passes (fig. 16), showing that not all of the leafhoppers fly into the cultivated areas during the spring dispersal.

In the southern section of the San Joaquin Valley, the beet fields were swarming with pale-green adults after the flight from the uncultivated plains and foothills had occurred. An examination of the vegetation in the Conner beet districts showed that there was a scarcity of annual saltbushes at the time that the invasion of the pest occurred, and this may account for the enormous congregation of the leafhoppers in the beet fields. During 1918, saltbushes made a normal growth, but in the spring of 1919, the saltbushes in the same localities, except in irrigated fields, made only a short growth and died, owing to a dry season.

When the immense swarms of beet leafhoppers flew into the cultivated regions on April 14, 1919, they were found during the next day generally distributed on green vegetation, but later they congregated on their most favorable host plants for the purpose of feeding and egg-laying. Large numbers of pale-green adults were found during the

Fig. 15. Summit of Panoche Pass, showing overgrazed hills sparsely covered with pasture vegetation, the most favorable habitat of the beet leafhopper.

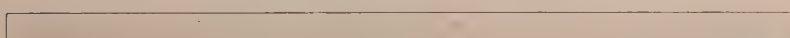


Fig. 16. Redscale or red orache (*Atriplex rosea* Linn.), growing in a mountain pass. After the spring dispersal the beet leafhoppers are generally distributed on annual saltbushes in the foothill regions, showing that not all of the leafhoppers fly into the cultivated areas.

spring on Russian thistles and different species of saltbushes, but these same plants were dry in July except in irrigated fields.

A few days were spent in the field to determine the northern boundary of the swarm. With the assistance of W. J. Hartung and the fieldmen of the Spreckels Sugar Company, the limit of the northern flight was found to follow roughly the Tuolumne River. The pale-green adults

Fig. 17. Stream lines showing movement of air from sea over California. (From H. R. Byers.)

were taken in beet fields and on other host plants from the Coast Range to the foothills of the Sierra Nevada Mountains, a distance of about 50 miles.

A few pale-green adults were taken in the beet fields at Manteca on April 19, 1919, but they were very abundant in the northern San Joaquin Valley on April 28.

In years between outbreaks there was a gradual increase of the leafhoppers in beet fields and on favorable weeds in the northern San Joaquin Valley, indicating that a succession of northward flights occur in the cultivated areas sometimes after the pasture vegetation becomes dry

on the foothills. The prevailing winds in the San Joaquin Valley are northwest (fig. 17) and apparently the insects fly against light northwest winds during their succession of northward flights, although calm spells often prevail at sunset.

During 1922 Schwing[26] reported that the spring flights which occurred on April 21 from the Panoche hills extended as far north on April 23 as French Camp, a distance of about 85 miles.

According to Schwing,[5] a high population of beet leafhoppers occurred in the middle San Joaquin Valley during the spring of 1929 and were carried by northerly winds toward the Tehachapi Mountains, and hence a low population of the insects occurred in the Sacramento Valley. The winds were continually blowing from the north, northeast, and northwest during May, carrying the leafhoppers into the southern San Joaquin Valley.

Spring Migrations

Into Sacramento Valley.—The appearance of the beet leafhopper in the Sacramento Valley is associated with a spring migration from the San Joaquin Valley. Fogs moving through Carquinez Strait may delay the migration of the leafhoppers into the Sacramento Valley. During the spring evenings a high fog frequently extends across the northern San Joaquin Valley. During foggy days the leafhoppers are sluggish and inactive, and when fogs occur before sunset no activity is displayed by the adults.

Schwing[27] found a gradual increase of the leafhopper on saltbushes in the northern San Joaquin Valley before, and a marked decrease after a migration into the Sacramento Valley.

The large migratory flights of the leafhopper into the Sacramento Valley usually occur in May, while the spring dispersal from the foothills into the cultivated areas of the northern and middle San Joaquin Valley occur in March or April. During the 1919 outbreak of the pest, the first large flights of the spring dispersals from the uncultivated plains and foothills into the cultivated regions of the San Joaquin Valley occurred on April 14 in the middle section and on April 28 in the northern section. In 1925 the spring dispersal was unusually early; the first flights occurred on March 29 and April 18, in the same parts of the valley.

Flights of small numbers of leafhoppers precede the large migration into the Sacramento Valley. The flights of the leafhopper during the 1925 outbreak, observed by Severin and Schwing[38] will serve as an

[5] E. A. Schwing, in a typewritten report to the Spreckels Sugar Company.

illustration. The first record of the spring migrants during 1925 was obtained in the inland beet fields of the Sacramento Valley on April 29. The leafhoppers were generally distributed but very scarce in the island or delta country on May 2. A large flight of the pest occurred on May 13, with variable winds from the south, southwest, and southeast blowing on May 11 to 13. No marked increase of the spring migrants occurred in the beet fields after May 22. The increase in the numbers of insects in the beet fields from May 14 to 22 was probably by short flights from unsuitable to favorable food and breeding plants. During 1925 Schwing observed a flight of the spring migrants in the beet fields near the city of Sacramento. The leafhoppers were flying everywhere and were settling on beets at dusk about 7 : 00 P.M. on May 13.

During 1922 to 1931 the maximum spring migrations into Sacramento Valley occurred on the following dates as determined by Schwing: 1922, May 25; 1923, about May 25; 1924, May 15; 1925, May 13; 1926, May 4; 1927, May 12; 1928, May 8; 1929, May 17; 1930, May 5; and 1931, April 26. In all of these years small migratory flights occurred before the maximum spring migration of the pest into the Sacramento Valley.

Across Suisun Bay.—During the 1925 outbreak, the beet leafhoppers probably flew across Suisun Bay to the beet fields near Suisun and Napa.

Lund[6] believed that the prevailing southwest winds from Suisun Bay blew the leafhoppers away from the island or delta regions toward the inland districts. It was assumed that the effectiveness of the winds against leafhopper invasion formed a triangle with the apex at Suisun Bay and the base extending roughly from Lisbon at the north, through Thornton and King Island at the south.

Carquinez Strait plays an important rôle in the direction of the wind. In the Sacramento Valley southerly winds prevail, but they are usually rather weak. The reason that Sacramento has southerly winds, while Stockton, 48 miles to the southward, has northwest winds, is that the former is north of Carquinez Strait and the latter south of it. The movement of the winds from Carquinez Strait is from the southwest toward the inland districts of the Sacramento Valley (fig. 17).

According to Mr. N. R. Taylor, of the United States Weather Bureau Office at Sacramento, the winds from Suisun Bay are of maximum velocity from 4 P.M. to midnight, decrease after midnight, and are of least velocity during the early morning hours. Calm days are rare in the Suisun Bay region during April and May, the months in which the migrations of the beet leafhopper into the Sacramento Valley occur.

[6] C. T. Lund, formerly Agriculturist of the Alameda Sugar Company, in a personal interview with the author.

When the leafhopper migrates northward from the San Joaquin to the Sacramento Valley, the relation of the direction of the wind in the San Joaquin Valley to calm days in the vicinity of Suisun Bay probably is important. Variable winds, such as northeast, south, or west, occur in the San Joaquin Valley when it is calm in the Suisun Bay. South winds, however, do not often blow in the San Joaquin Valley during April and May. When the sea breezes from San Francisco and Suisun bays strike the Sierra Nevadas, the winds are deflected to the north, creating a south wind in the Sacramento Valley, and to the southeast, resulting in a northwest wind in the San Joaquin Valley, and these winds prevail during the spring and summer.

Before the enormous hordes of leafhoppers migrated into the Sacramento Valley during the spring of 1925, Severin and Schwing(38) stated that there seemed to be no reason, with the information at hand from the Weather Bureau office, why it would not be possible for the leafhopper to invade the island or delta districts in large numbers during the spring migrations if conditions are favorable in certain years.

During the spring of 1925 a high population of beet leafhoppers occurred on the uncultivated plains and foothills in the middle San Joaquin Valley, but the pasture vegetation dried up rapidly in the southern part of the valley, and the population there was reduced. A severe outbreak of the pest occurred in cultivated areas of the San Joaquin and Sacramento valleys. During the spring of 1926 a high population occurred in the southern San Joaquin Valley and a low population in the middle section of the valley. A fairly low population of leafhoppers invaded the Sacramento Valley. It was assumed, therefore, that the origin of the pest in the Sacramento Valley is from the middle and northern San Joaquin Valley rather than from the southern part.

A peculiarity noted during the spring of 1926 was that a higher population of leafhoppers occurred on the Holland Land tract in the vicinity of Courtland than in any other locality in the Sacramento Valley. Fifty acres were plowed under owing to curly top on the Holland tract, but early-planted beets were not seriously affected by the disease. There were 600 acres of beets on Jersey Island, bordering the southern bank of the San Joaquin River, but the leafhoppers were extremely scarce in the beet fields. In the northern San Joaquin Valley the leafhoppers were abundant, and 50 acres of late-planted beets grown in Union Island were plowed under. It is difficult to explain the invasion of a high population of insects on the Holland Land tract by wind directions.

On April 14, 1921, the beet leafhoppers flew into the cultivated areas of the northern San Joaquin Valley and extended as far north as Wood-

land in the Sacramento Valley on April 15, but no specimens were taken in the Meridian beet fields about 30 miles north of Woodland on April 16, nor on April 30. A low population of leafhoppers occurs on the foothills from the Altamont Pass to the northern limit of the natural breeding grounds. If the flights into the cultivated areas started from the northern canyons in the San Joaquin Valley, the distance to Woodland would be approximately 60 miles. Leafhoppers have been taken on nettle-leaf goosefoot (*Chenopodium murale*) as far north as Red Bluff[28] in the northern extremity of the Sacramento Valley. The distance from the vicinity of the northern San Joaquin canyons to Red Bluff, probably covered in successive northward migrations following the cultivated areas, would be 150 miles.

There is no evidence to show that a return, autumn, southward migration of the beet leafhopper occurs from the Sacramento to the San Joaquin Valley. The slow southeastern flights parallel to the foothills at sunset in the San Joaquin Valley are movements within the natural breeding areas, and may be associated with the search for a favorable canyon or mountain pass or for food, or with mating or peculiar light reactions.

Into Livermore Valley.—It has often been suggested that the beet leafhoppers migrate from Corral Hollow through the Patterson Pass into Livermore Valley, situated between the Inner and Outer Coast ranges. Niles and Dublin canyons and the Altamont Pass open into this valley. Leafhoppers are scarce during the spring on the foothills bounding Altamont Pass and on the foothills toward the northern limit of the natural breeding grounds near Pittsburg. No nymphs have been found on the foothills bounding Livermore Valley.

Into San Francisco Bay Districts.—When a low population of the beet leafhoppers occurs in the natural breeding areas, curly top rarely occurs in the San Francisco Bay districts. During the spring of 1927 a migration of the pest into the San Francisco Bay districts occurred, probably from the San Joaquin Valley; in that year about 5 per cent of the tomatoes were infected with curly top in the districts east of the regions between San Francisco and Monterey bays. Tomatoes were also infected with curly top in the Hayward district during the 1919 and 1925 outbreaks of the leafhopper. During the spring of 1930 an occasional leafhopper was taken on common yellow mustard (*Brassica campestris*) near Pinole.

During the 1919 and 1925 outbreaks of the leafhopper, beets planted at Berkeley were all infected with curly top. Mangelwurzel, or stock beets, planted during April at Berkeley were also found to be naturally

infected with curly top.[37] During 1927, 1931, and 1932 the pest migrated into the fog belt of the San Francisco Bay district, and beets planted at Berkeley were again infected with curly top. An occasional leafhopper was taken east of the Berkeley hills during the spring of 1931. In all probability the flights of the leafhoppers were associated with southeast winds, spreading the insects into the San Francisco Bay districts from the San Joaquin Valley.

Across San Pablo Bay.—During the 1925 outbreak of the beet leafhopper the insects were present in the sugar-beet fields at Ignacio, crossing the San Pablo Bay in their spring migratory flights.

Into Santa Clara Valley.—Spring migrations of the beet leafhoppers occurred into the Santa Clara Valley during 1919, 1925, and 1927. Curly top of sugar beets was more severe towards the upper end of the valley. Tomatoes were also infected with curly top in these same years. In years between outbreaks an occasional curly top beet was found, indicating that a low population of the pest invades this valley. The leafhopper has been found breeding in rocky localities near Coyote and Lick in the Santa Clara Valley, but this is a minor and temporary breeding area. In years of abundance the insect probably migrates northward in the Santa Clara Valley from the foothills extending from the Santa Ana Valley to the western entrance of Panoche Pass.

Into San Juan Valley.—Schwing[26] reported that March and April plantings were destroyed by curly top on one side of the river in the San Juan Valley while on the opposite side of the river May plantings produced a good crop during 1921. The San Juan Valley is a continuation of the Santa Clara Valley, and the origin of the beet leafhopper in both valleys is probably the natural breeding area extending from Santa Ana to the western entrance of Panoche Pass. Migrations into both valleys probably occur from the San Joaquin Valley.

Into Salinas Valley.—It has been observed by Hartung[18] that when south winds blew in the Salinas Valley during April or May, the beet leafhoppers were found in the beet fields in the fog belt. He also noted that when winds blew from the east, southeast, or south, fogs were usually absent in this valley.

During the dry season the trade winds entering the Salinas Valley from Monterey Bay during the forenoon blow with increased force as the upper or narrow portion of the valley is approached. Northwest winds prevail throughout the entire season (fig. 17). Their maximum velocity is usually reached in the early afternoon, and as evening approaches they gradually decrease in force and nearly or quite cease during the night. The spring flights of the leafhopper from the foothills

into the cultivated areas probably occur during the evening or at night when the brisk winds cease blowing.

During the dry season the fogs arise from the sea, sweeping through Monterey Bay and encroaching upon the land very suddenly. The spring migrations into the fog belt from the upper end of the valley apparently are associated with southeast winds and occur when fogs are absent in the Salinas Valley.

The spring flight from the semiarid breeding centers to the fog-belt districts must be considered a migration. No return flights occur from the coastal regions to the natural breeding areas.

For many years the evidence was lacking that the leafhopper migrated from the San Joaquin into the Salinas Valley. The fact that the leafhoppers after the spring dispersal are found on favorable weeds growing along roadsides and in cultivated areas in mountain passes is no evidence that the insects migrate through the mountain passes. There used to be a large alkali sink near Bitterwater and another near Cholame covered with annual saltbushes on which the insects were found during the spring, summer, and autumn. When red-stem filaree became dry on the foothills the insects left the plants and assembled in the mountain passes on favorable food and breeding plants, on which the summer and autumn generations developed.

A sudden increase in the number of leafhoppers in the beet fields may be associated with a large flight from the foothills of the Salinas Valley. When the period of the spring dispersal from the natural breeding areas in the Salinas Valley is considered, and a concentration of leafhoppers in a valley from 7 to 9 miles in width and beet fields scattered from King City to Monterey Bay, a distance of 53 miles, a relatively low population on the foothills may result in a high population in the beet fields, especially outside of the fog belt.

During the period of 1918–1921, the first appearance of the pale green adults of the spring generation in the cultivated areas of the Salinas and San Joaquin valleys was as follows:

Salinas Valley	*San Joaquin Valley*
1918: May 8, King City	1918: April 24, upper
1919: April 2, King City	1919: April 8, 14, 28, upper, middle, lower
1920: April 22 to 23, King City	1920: April 23, upper
1921: April 25 to 30, King City	1921: April 6, 14, upper, middle

During the spring of 1920 the flights in the San Joaquin and Salinas valleys occurred at the same time, but during 1918, 1919, and 1921 the flights in the San Joaquin were earlier than in the Salinas Valley.

During the spring of 1922, Schwing[7] was convinced that the beet leafhoppers migrated from the San Joaquin into the Salinas Valley. The seasonal rainfall at the Spreckels ranch near King City was 13.15 inches[8] and the monthly rainfall was as follows: September, 0.15; October, 0.12; November, 0.28; December, 5.33; January, 3.36; February, 2.26; March, 1.09; April, 0.28; and May, 0.28 inches. The winter was unusually cold. He failed to find the leafhopper on the foothills near King City, San Ardo, Bradley, and Indian Valley and none were found on early-planted beets in the cultivated areas. A survey of the Panoche hills showed that few leafhoppers had acquired the winged stage on April 17, but in early May a high population occurred on these same hills. An enormous spring migration of leafhoppers must have occurred from the San Joaquin into the Salinas Valley on May 15; from 20 to 100 adults to 100 feet of beet row were estimated on May 16–17 in the beet fields near King City, Greenfield, Soledad, Gonzales, and Chualar.

During the spring of 1925 two large flights of the leafhoppers occurred in the Salinas Valley. The leafhoppers were abundant in the beet fields in the interior regions and fog belt of the Salinas Valley on March 27. As stated in a previous paper,[(38)] the early development of the spring generation was associated with a warm dry winter. The pasture vegetation became dry in January except on the north slopes of the eastern foothills in the upper Salinas Valley. The root system of red-stem filaree (fig. 18) was not destroyed by the drought, and this plant became green again after early February rains. A dry period occurred from February 22 to March 26, with a limited amount of rainfall—0.11 inches on March 9 and 10. The early flights in the Salinas Valley between March 24 and 26 were probably associated with the second drying of the pasture vegetation.

A second large flight occurred into the Salinas Valley on April 12, and the insects were also found in the San Felipe and Watsonville beet fields. After the second large flight occurred, a thorough search failed to reveal the presence of a single nymph on the eastern foothills bounding the Salinas Valley. Pale-green adults of the spring generation were found in all canyons and mountain passes examined from Chualar to San Miguel. In Chualar Canyon and Gloria Valley, situated in the fog belt, adults were taken, but no nymphs have ever been found in them. The fact that the adults were found on the foothills within the fog belt seems to indicate that a migration occurred from the San Joaquin Valley. In the mountain passes between King City to Bitterwater and

[7] E. A. Schwing, in a personal interview.

[8] According to the United States Department of Agriculture Weather Bureau station at King City, 12.12 inches was the seasonal rainfall.

Fig. 18. Red-stem filaree (*Erodium cicutarium*) showing long taproot. During a dry spell in February and March the foliage becomes dry, cutting off the food supply of the nymphs, but after late spring rains, plants with long taproots may develop leaves again.

San Lucas to Coalinga, also in Reliz Canyon near Greenfield, and Pancho Creek near San Ardo, low-flying specimens were observed during the morning before the heavy winds began to blow.

Another trip was taken to the Salinas Valley on April 27–29. In Chualar Canyon only 7 adults were taken during one half day. The adults were still abundant in canyons and mountain passes outside the fog belt but no nymphs were found. Nymphs, however, were bred in the greenhouse from eggs deposited in red-stem filaree removed from canyons and mountain passes. Late spring rains fell during March, April, and May in the Salinas Valley, and the pasture vegetation which normally becomes dry during April or May remained green until June. A partial second brood developed on the foothills from eggs deposited by the migrating insects.

During the spring of 1927 the evidence indicated that the beet leafhoppers migrated from the San Joaquin into the Salinas Valley. The first warm days for several weeks occurred on April 20 and 21, and the pasture vegetation had dried considerably on the foothills in the middle San Joaquin Valley. Schwing observed, on April 21, short flights on the foothills in the vicinity of Coalinga, and during the daytime on the Cantua hills and in Big and Little Panoche passes. During the early evening on April 21 a light east wind was blowing which later changed to southeast.

According to Schwing,[9] the adults of the spring generation were not found on April 20 on favorable host plants growing in the cultivated areas near Manteca, Turlock, Merced, Chowchilla, and Fresno. During the afternoon and early evening on April 21, no leafhoppers were taken on saltbushes, Russian thistle, and lamb's quarters (*Chenopodium album*) from the Panoche hills to Merced, and east of Oro Loma. A return trip was made from Merced to Oro Loma on April 22, and the leafhoppers were taken on favorable weeds which had been swept during the previous day. An examination of Little and Big Panoche passes showed that a large flight had occurred from these mountain passes.

The leafhoppers flew with east winds from the San Joaquin into the Salinas Valley on April 21, 1927. Schwing sent the writer a telegram on April 21, stating that they were congregating in the entrance of Little Panoche Pass and that east winds would probably carry them into the Salinas Valley. The next morning leafhoppers were found basking in the sunshine on the upper surface of the beet leaves at King City. A very low population of the insects occurred on the eastern foothills bounding the Salinas Valley previous to the migration.

[9] In a typewritten report to Spreckels Sugar Company.

There are two possibilities in regard to the paths of the migratory flights from the San Joaquin into the Salinas Valley: the leafhoppers flew either through the mountain passes or over the Inner Coast Range and the Gabilan Mountains. The general distribution of the leafhoppers in the canyons and mountain passes from Chualar Canyon to San Miguel during 1925 indicates that a mass movement of enormous hordes of leafhoppers from the uncultivated plains, canyons, and foothills in the San Joaquin Valley took place over the mountain ranges into the Salinas Valley.

Into Southern Counties.—During the 1919 outbreak of the beet leafhopper, spring migrations occurred in all of the principal beet centers located in the fog belt of San Luis Obispo, Santa Barbara, Ventura, Los Angeles, and Orange counties. In regions outside of the fog belt the insects were abundant and curly top was severe.

An outbreak of curly top occurred in the territory of the Union Sugar Company during 1925 and it was estimated that about 25 per cent of the crop was lost. The leafhoppers invaded the beet fields during 1922, 1926, and 1927 but no serious losses from curly top were sustained.

Although it was assumed that the leafhoppers migrated from the southern San Joaquin Valley into the coastal regions of these southern counties, no accurate mapping of other natural breeding areas has been attempted up to the present time.

Method of Migration.—According to Carter[9] "The appearance of the insect in areas separated from its natural breeding ground by high mountain ranges cannot readily be explained by a teleological theory of migration. The insect is extremely small and of light weight, and the slightest ground breeze will carry it for yards. It does, however, migrate, and should it encounter strong winds it is quite conceivable that it might be blown into upper air currents and by them be transported (in what must practically amount to cold storage, since these upper air currents are often of very low temperature) for long distances."

In California upper-air soundings have been made by airplane and in sounding balloon ascensions. There is conclusive evidence that along the coast there exists an upper stratum of warmer and relatively drier air. Air soundings have been made by airplane at the naval station on North Island, San Diego Bay, since January, 1923. The results of 35 afternoon flights during July and August, 1924, indicate according to Blake[3] that there is a decrease in temperature up to 500 meters, then an increase up to 1,250 meters, and another decrease parallel with the first, from that altitude upward (fig. 19). Blake writes:

As anticipated, the lowest temperatures were reached at the average level of the top of the clouds, the decrease for the first 500 meters averaging 0.6° C per 100 meters, or 0.4° C less than the adiabatic rate of dry air. From 500 to 1,250 meters a rise of 7.2° C is shown, and from 1,250 meters on the temperature fall is at the same rate as the initial decrease, or 0.6° C for each 100 meters. Surface temperatures corresponded generally with those found at 1,800 or 1,900 meters.

Naturally the relative humidity and temperature curves parallel each other rather closely but in an inverse sense [fig. 19].

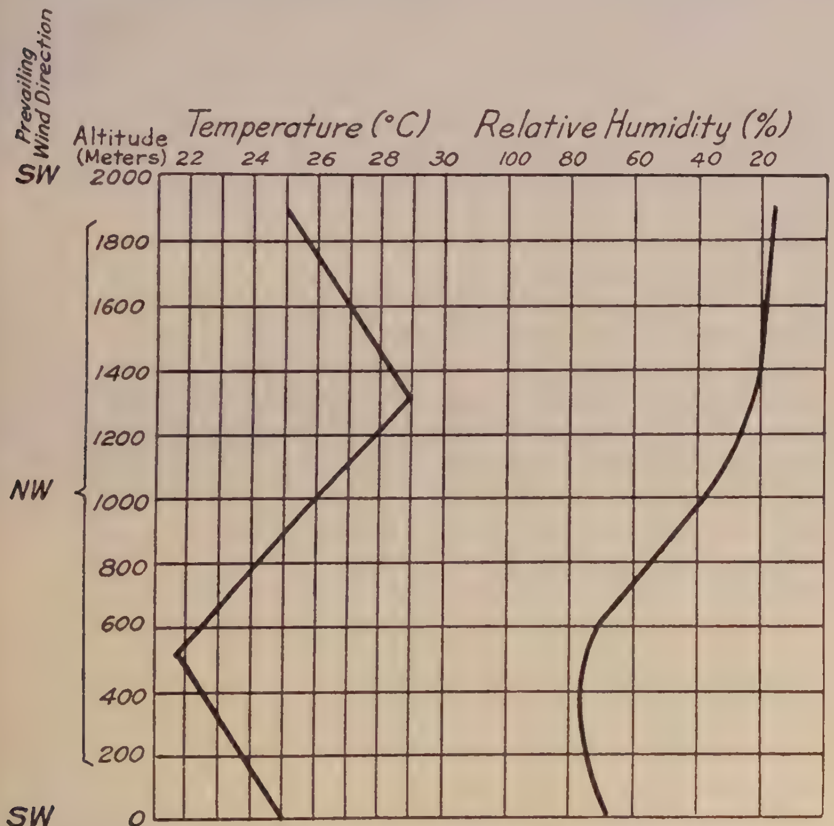


Fig. 19. Curve of average vertical temperature and relative humidity distribution during summer months over San Diego. (After D. Blake.)

Byers[6] in flying over the Santa Clara Valley and Monterey Bay during midafternoon at an altitude of 1,400 meters and in passing over the Santa Cruz Mountains experienced no cooling off. The descent to land at Oakland produced a sensation similar to stepping into a refrigerator. The temperature on land was 17° C, and a moist breeze was blowing at a moderate rate from the west.

Anderson[1] states that "during the summer the inversion ordinarily extends from southern Washington to a point 800 to 1,000 miles south of San Diego, west from the coast for a distance of 200 to 300 miles, and over the land areas between the ocean and the Coastal Range."

Blake[10] states:

> The eastern limit of the summer temperature inversion here in the south is not fixed, and the extent of the stratum varies not only with topography, but also with the changes that take place in the controlling weather factors. At times the cloud layer, which is used as an index to the extent of the stratum of cooler air from the ocean, is found a short distance only over the land, while again it penetrates some distance over the valley into the mountains.
>
> I think that it may be assumed that in central California the inversion will be found usually extending to the Coast Range, and at times penetrating through the passes you have mentioned [Pacheco, Little and Big Panoche, Coalinga—King City, and Cholame].
>
> Beyond the Coast Range, the descending currents on the lee side give rise to dynamical heating and the inversion is not possible. For this reason it is almost certain that the inversion common to the coast will not be found as such as far inland as Stockton, but might reach at times to Antioch.

Byers[11] wrote as follows:

> Your question concerning the vertical temperature distribution above the San Joaquin entrance to various passes in the Coast Range is almost impossible to answer because free air soundings are completely lacking in that region.
>
> Surface observations from that locality and also observations from Mount Hamilton and a few observations I have made in flying over this region indicate that during most of the day there is no well-defined inversion over the San Joaquin entrances, although it is usually well marked during the morning and night at the western ends of these passes. In the late fall, winter, and early spring during periods when there is no cyclonic activity, very strong inversions build up in all the valleys and canyons of the Coast Ranges and in the San Joaquin Valley as well. At this time there is no sea breeze, but the air is practically calm at the surface with a movement from east to west at higher levels. On numerous occasions temperatures of 50 to 60° F have been observed at Mount Hamilton when in the valleys all around it was near freezing.

The spring flights of the beet leafhopper have frequently been observed at sunset during calm evenings in the eastern entrance of Little Panoche Pass. The flights could be followed out of the entrance of Little Panoche Pass at sunset, but the flight of an enormous swarm out of the pass has never been observed. The flights appeared to be associated with ascending air currents at dusk. The ascending air currents

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[10] Blake, D., letter to the author dated February 15, 1932, in response to a question as to whether he believed temperature inversion occurred above the San Joaquin entrance of certain passes.

[11] Byers, H. R., letter to author dated February 16, 1932.

may carry some of the leafhoppers into the upper air stratum and here they may drift and fly long distances, possibly over mountain ranges. Their presence in the upper air could be determined by airplanes equipped with insect-collecting traps carried between the wings.[44]

According to Byers, a movement of the higher air from east to west occurs during early spring, when there is no cyclonic activity and the air is practically calm at the surface, and the leafhopper could readily be transported by the higher winds from the San Joaquin Valley into the Salinas Valley.

The following examples of migrations of the beet leafhopper in other states and islands may represent transportation of the insect by upper air currents rather than by surface migrations through successive flights from the natural breeding areas.

Ball[2] has found the beet leafhopper in abundance on the snow on Pikes Peak above 14,000 feet and has captured examples on the Beaver Mountains at 12,000 feet. They were swarming near Panguitch, Utah, at an elevation of 7,000 feet, just at the time the immense swarms swept over the beet regions of Utah in 1915.

Whirlwinds may have carried the leafhopper to these high altitudes or the insects may have been transported by the higher winds.

During 1926 Carter[9] found the beet leafhopper on the east side of the Continental Divide in Montana and a reasonable interpretation was that these specimens represent the few straggling individuals which had survived a long-distance migration. Migrations from the breeding grounds in Idaho and Washington probably occur into the Bitterroot Valley and Flathead (Kalispell) districts of Montana.

Severin and Severin[39] found that curly top of sugar beets occurred on rare occasions in the beet fields of the west-central part of South Dakota. Sweepings with an insect net from the most favorable host plants of the beet leafhopper failed to include a single specimen. It was demonstrated, however, that previously noninfective beet leafhoppers transmitted curly top from South Dakota diseased beets to healthy beet seedlings under greenhouse conditions in California. If the beet leafhopper was responsible for the diseased beets which were found in South Dakota, there is a possibility that the insects migrated into west-central South Dakota from regions outside of the state.

According to Ball[2] curly top of sugar beets has been reported from Nebraska and Kansas. In all probability Kansas and Nebraska are outside of the range of its natural breeding grounds and the beet leafhopper migrated into these states.

Carter[10] reported tomato curly top transmitted by the beet leafhopper in Muscatine, Iowa, as probably a case where the insect migrated out of its normal range into areas where it cannot survive.

De Long[12] collected nymphs and adults of the beet leafhopper in abundant numbers at Miami, Florida, on sea purslane (*Sesuvium portucastrum* L.) growing natively on the upper beach and sand dunes of the bays and inlets of the Atlantic Coast. They were collected during April, 1921. Ball visited the same localities in Florida in later years but failed to collect the leafhopper. Whenever the leafhopper migrated into the coastal regions of California it failed to establish itself. In all probability the leafhopper migrated to Miami, Florida, from the southwestern part of the United States or northern Mexico.

Henderson[20] failed to find the beet leafhopper on Isla Raza on May 16, 1928, whereas Van Duzee[45] captured many specimens on April 21 and May 4, 1921. A migration of the pest probably occurred from Lower California to Isla Raza during 1921.

Summer Dispersal in Sacramento Valley

An attempt was made to determine the longest distance that the adults of the summer generation flew to reach the late-planted beet fields in the Sacramento Valley during 1925. In many fields of unthinned and thinned beets examined in June, only a low percentage of curly top was present, owing to the fact that these beets had germinated after the flights of the spring migrants had ceased. The nymphs of the summer generation began to acquire the winged stage about July 1, and a gradual increase of the adults occurred in late May, June, and July plantings. One field of 100 acres of unthinned beets contained at least one leafhopper to each beet on July 14. There were no other beet fields within 15 miles on the north, east, or south; the nearest beet field was 3 miles to the west. The adults of the summer generation must, therefore, have flown at least 3 miles to the 100 acres of unthinned beets, although some of them probably invaded the late-planted beet fields from weeds growing in the vicinity. The flights may have been influenced by the prevailing winds from Suisun Bay. In all probability the flights of the adults of the summer generation from one beet field to another was associated with a food stimulus. An examination of the beet fields planted in March, April, and May showed that many of the beets had died owing to curly top. Extremely hot weather had scorched the outer leaves of the beets leaving a tuft of diseased, thick, leathery leaves.

Summer Migration from San Joaquin Valley

During the 1919 outbreak of the beet leafhopper, summer migrations from the San Joaquin Valley occurred. During the spring thousands of leafhoppers were found on various species of saltbushes in the southern San Joaquin Valley, but in July it was difficult to secure 100 adults on these same plants. In the Connor and Corcoran beet districts the sugar beets were mostly dead owing to curly top, but the adults were scarce on the green innermost leaves with dried outer foliage of such beets as could be found. Sweepings were made on some of the most favorable host plants, such as the saltbushes growing in and along the margin of beet fields, but the leafhoppers had not assembled on these plants.

In the middle San Joaquin the beet leafhoppers were extremely abundant on Russian thistles and various saltbushes during April, but in July the adults were rare on these plants. Along the roadsides and in the fields that had not been irrigated, Russian thistles attained a few inches of growth and died during the spring owing to a shortage of rain and probably also to the drain of enormous hordes of leafhoppers.

In the northern San Joaquin enormous numbers of adults had congregated on June 26 on *Atriplex bracteosa* growing among diseased beets in the vicinity of Hatch Station. The foliage of these saltbushes was covered with droplets of clear excrement which glistened in the sunshine. When a person walked past one of the weeds, so that a shadow was thrown on the plant, a swarm of leafhoppers flew up. Nymphs were still abundant on sugar beets with green innermost leaves and dried outer foliage. The next visit to these beet fields on July 5 showed that most of the insects had left the saltbushes and that a summer migration had occurred. Another assemblage of leafhoppers was observed on *A. bracteosa* on July 26.

Autumn Dispersal

In San Joaquin Valley.—The earliest record of the return flights to the foothills of the Coast Range in the northern San Joaquin Valley was on October 8, 1919, before the pasture vegetetion germinated. During 1919 the plants and foothills were not covered with green pasture vegetation until after the rains fell on December 1 to 6. A few adults were taken in each sweeping on Bermuda grass (*Cynodon dactylon*) growing along a creek in a canyon. An occasional specimen was taken on tarweed (*Hemizonia virgata*) and on *Eriogonum angulosum.*

In the middle San Joaquin Valley the adults were captured during October, 1919, on perennial plants growing on the uncultivated plains and in canyons and mountain passes. The insects were also taken in large depressions and squirrel holes on the plains, where the insects probably sought the shade.

During November, 1919, the autumn dispersal of the leafhoppers to the foothills was at its maximum in the northern and middle San Joaquin Valley. The insects were most abundant on perennial plants growing in canyons and mountain passes. In canyons perennials were usually abudant in dry streamways, tributaries, and drainage furrows. Specimens were also taken on tree tobacco (*Nicotiana glauca*) and pepper trees (*Schinus molle*).

An attempt was made to study the movements of the leafhopper near and in the entrances of canyons in the northern San Joaquin Valley, but only an occasional specimen was captured flying south about 3 to 4 feet above the surface of the ground. The windshield of an automobile facing the setting sun attracted dozens of adults, which exhibited a peculiar sexual behavior.[29] The automobile was stationed about $\frac{1}{2}$ to 1 mile outside the mouth of various canyons, and in every case the leafhoppers settled on the machine in a few minutes. Several miles from the foothills, the leafhoppers were attracted to the auto in stubble fields, plowed fields, and in a graveled road between two plowed fields where no green food was available. The reflected light rays from the setting sun on the windshield may have attracted either the higher-flying insects moving from the cultivated areas to the foothills, or possibly those which had settled on the ground before reaching the foothills, since low-flying specimens were rarely taken on the wing.

In the northern San Joaquin Valley cultivation often extends to the base of the foothills and occasionally to the hills; hence a more favorable locality to study the flights was found in the middle section of the valley, where the plains and foothills are covered with pasture vegetation. Whenever the automobile was stopped on the plains so that the windshield faced the setting sun, the adults assembled on the car and the pairing of the sexes was observed. By sweeping with an insect net an occasional specimen was captured in the dry pasture vegetation growing on the plains. When the hillsides became partly shaded, dozens of low-flying leafhoppers could be plainly seen slowly flying southeast down the valley following the general direction of the foothills. No similar movement of leafhoppers was observed on the plains (fig. 20, *P*) from $1\frac{1}{4}$ to 3 miles away from the foothills nor in the cultivated areas. The flying leafhoppers appeared white in color and hence could be dis-

tinguished easily from the multitude of other insects hovering in the air at sunset. In the sunshine they became invisible about 15 feet above the surface of the soil where a background was lacking.

The flights of the leafhoppers were also studied on November 11 to 13, 1919, in Wild Cat Canyon, situated about 5 miles west of Oro Loma, where they were extremely abundant. When the sun warmed the foothills occasional specimens were observed on the wing at about 11 A.M.

Fig. 20. Wild Cat Canyon, 5 miles west of Oro Loma. SE, southeast foothill; NW, northwest foothill; P, plains, showing perennials which serve as food plants of the beet leafhopper during dry autumns, before the pasture vegetation has germinated. After the pasture vegetation germinates the beet leafhoppers leave the perennials and are found on red-stem filaree (*Erodium cicutarium*) growing on the plains and foothills.

in the mouth of the canyon, where they flitted about here and there, probably in search of food. At 4:30 P.M. the adults were common in the air, and at 5 P.M. the activity was at its height and continued until shortly after sundown. The flights of the insects could be seen across a dry creek with the southeastern foothill (fig. 20, *SE*) bounding the entrance of the canyon as a background. Some of the leafhoppers flew across the sunny canyon, and when they entered the shadow of the southeastern foothill, they settled to the ground; others flying higher continued southeast along the Coast Range. The foothills situated on the southeastern side of the entrance to the canyon were higher and projected out farther than the northwest hill (fig. 20, *NW*), and as the sun was sinking behind the mountains the former became shaded sooner

and the latter cast a larger shadow on the plains. An examination of the southeastern foothills showed that the leafhoppers were abundant in dry pasture vegetation and on perennial shrubs, on which the sexual behavior was observed. A striking peculiarity was the fact that they were common on dry pulverized soil along the steep banks of the creek. Enormous numbers had assembled on *Atriplex polycarpa* growing on the banks and bottom of the creek. Investigations were made 1 mile up the canyon, and the same relative abundance was found on different species of plants. The leafhoppers were frequently observed flying south in the sunny canyons.

The leafhoppers do not fly in the vicinity of the foothills or canyons on cloudy days or when heavy winds are blowing. On November 18, the sky was overcast by dark clouds at 4 P.M., and it remained cloudy until near sunset, when it cleared for a few minutes at intervals. When the sun was shining, the canyon soon became warm, and occasional leafhoppers were observed on the wing. They were attracted to the automobile, but when the sun was hidden behind the clouds, the temperature dropped and they settled to the ground.

During the autumn dissemination a southward movement toward the foothills was observed by an occasional low-flying leafhopper. Specimens attracted to the automobile were captured during the autumn flights in the cultivated areas, and when they were liberated the general direction of flight was southerly towards the foothills in the northern part of the valley. The insects were set free during an apparently calm spell, but when a handful of dust was thrown into the air, the compass indicated that the particles were carried in a southward direction. Similar tests were made on the plains in the middle of the valley; there the insects flew south when a north breeze was blowing, or southeast with a northwest breeze.

During the autumn leafhoppers fly into the eastern and western entrances of mountain passes in the Inner Coast Range. In the autumn of 1919, they were found in the eastern and western entrances of the Altamont and Cholame passes. In the autumn of 1925 they were commonly taken in the western entrance of Panoche Pass near Paicines. In the spring of 1925 and 1926 nymphs were abundant for a distance of about 5 miles in the western entrance of Panoche Pass.

During October and November the activity of the leafhoppers is probably aroused by a lowering of the temperature at sunset, but during December flights have been observed during the morning and afternoon. During the autumn they have frequently been observed flying against light breezes in canyons and mountain passes. A study of the flights

at the mouth of canyons indicates that air currents blowing out of the canyons at sunset are probably not the only stimulus which causes the leafhoppers to fly into the canyons, because many of the insects flew past the entrance and followed the contour of the hills or settled to the ground when they entered the shade. Light reactions at sunset may also play a role in guiding them into canyons and mountain passes. The windshield of an automobile attracted hundreds of leafhoppers at sunset; they resembled the swarming of enormous numbers of insects around an electric arc lamp.[29]

In Sacramento Valley.—An autumn dispersal of the beet leafhoppers from the cultivated areas to the foothills of the Inner Coast Range occurs in the Sacramento Valley. In years when an outbreak of the pest did not occur, a low population of dark overwintering adults were found in small valleys and canyons located in the eastern foothills of the Coast Range bounding the western side of the Sacramento Valley. In the southern part of the Sacramento Valley, the Montezuma and Yolo hills are mostly cultivated, and the foothills west of Winters are covered with orchards and are not favorable winter quarters for the leafhopper. After the 1925 outbreak of the pest, the insects were taken on red-stem filaree and weeds growing on the foothills of Vaca and Capay valleys and in canyons west of Dunnigan, Williams, Maxwell, and Willows. The dark overwintering forms were also taken on red-stem filaree growing on the west side of the Marysville Buttes.

An investigation was also conducted on the foothills of the Sierra Nevada bordering the eastern side of the Sacramento Valley. The foothills are often rolling or merely undulating, and the timbered region is soon reached after leaving the valley slopes. The leafhopper was rarely taken during the autumn on the foothills. Red-stem filaree is not abundant on the hills and there is no indication on this side of typical beet-leafhopper foothill breeding grounds. The locations investigated in the Sierra Nevada foothills were: 7 miles northeast of Red Bluff; 10 miles east of Chico; vicinity of Oroville; 12 miles east of Marysville; vicinity of Newcastle; and vicinity of Ione.

In Salinas Valley.—In the Salinas Valley the return flights of the dark overwintering adults follow the Salinas River and its tributaries flowing from the Gabilan Mountains bounding the east side of the valley. With the approach of the rainy season the trade winds gradually decrease in force. During November there are occasional days with calm evenings when the autumn flights of the leafhopper to the foothills have been observed. Short flights from perennial to perennial were observed in the canyons. The movement of the leafhoppers from salt-

bushes covering a large alkali sink in a mountain pass at Bitterwater was not eastward toward the Inner Coast Range but westward into the Gabilan Mountains.

A blanket of fog usually covers the base of the foothills of the Sierra Santa Lucia Range as far south as Greenfield, a factor which is unfavorable to the overwintering adults.

Stimuli of Dispersal and Migration

The spring-dispersal flights of the beet leafhopper are probably associated with a food stimulus; the adults fly from the uncultivated plains and foothills after the pasture vegetation becomes dry and invade the cultivated areas when the annual saltbushes are succulent and most favorable from the standpoint of food and egg deposition. The autumn flights of the leafhopper are probably also associated with a food stimulus; the insects fly from the cultivated territory when the saltbushes and other favorable weeds become woody and dry. In the Salinas Valley, however, the dark overwintering adults left large beets and even small beets in experimental plantings during 1919, indicating that the autumn flights will occur regardless of whether favorable food is available or not.

There does not seem to be any consistent relation between reproductive stimuli and the spring and autumn dispersals of the leafhopper. After the spring dispersal about 8 per cent of the spring-generation adults that invaded the cultivated areas in the middle San Joaquin Valley were males and 92 per cent females. Most of the males remain behind on the uncultivated plains and foothills and are common on perennials after the pasture vegetation is dry, but are rarely taken during the summer and probably die. Dissections of females after the first spring flight into the cultivated areas had occurred showed that 92 per cent had mature eggs in the ovaries. During the autumn flights, however, most of the males follow the females to the uncultivated plains and foothills, and mating occurs during the autumn. The dark overwintering females are not at the egg-laying stage during the autumn dispersal; dissections of specimens collected in canyons of the Coast Range in the northern and middle portions of the San Joaquin Valley at intervals showed the following average percentage at the egg-laying stage: December, 4 per cent; January, 52 to 64 per cent; and February, 86 to 99 per cent. The males die during the winter. It is difficult to associate the mating and egg-laying stimuli with the spring and autumn flights of the leafhopper.

The stimulus for summer migrations of the adults is probably hunger, owing to overcrowding. As already mentioned, the sugar beets in the southern section of the San Joaquin Valley in 1919 were mostly dead as a result of curly top. The most favorable host plants were stunted and dry, except in irrigated fields, and yet the adults had not assembled on these plants in irrigated fields. The leafhoppers, however, will leave green succulent plants in the Imperial Valley, without an apparent stimulus as reported in previous papers.[28, 30]

NATURAL BARRIERS

In San Joaquin Valley.—During the autumn dispersal of the beet leafhoppers from the cultivated areas to the foothills, large numbers of adults often congregate during dry autumns on perennials growing in canyons in the northern San Joaquin Valley. When the populations of leafhoppers during the autumn and spring on the northern foothills and in canyons were compared, it was evident that a marked reduction of the spring generation occurred during a normal season of rainfall. After the 1919 and 1925 outbreaks of the pest a marked decrease in population of the spring generation occurred compared with the autumn generation in the Altamont and Pacheco passes.

In the San Joaquin Valley rainfall decreases from north to south, and with minor exceptions is considerably less on the western side of the valley than on the eastern side. Stockton, in the northern part of the San Joaquin Valley, has an annual rainfall of 14.35 inches, while Bakersfield, in the southern part of the valley, has 5.68 inches. Table 3 gives the annual rainfall of towns on the western and eastern sides of the valley.

Heavy rainfall kills some of the leafhoppers. At Manteca 3¾ inches of rain fell on September 11 to 13, 1918, before the return flight of the insects to the uncultivated plains and foothills had begun. In sugar-beet fields dead adults with wings spread were observed partly embedded in sandy soil below the leaves of diseased sugar beets and also in the folds of dried beet leaves. Dead leafhoppers partly embedded in the soil were also commonly taken below branches of *Atriplex bracteosa*, where they evidently crawled to escape from the rain. Dead nymphs were rarely found, but if present they would probably have been difficult to detect. An examination of the adults under a binocular microscope showed that 50 per cent had been parasitized. The material was dry and could not be dissected to determine whether the remaining 50 per cent were not weakened forms that had parasitic larvae within their

bodies. Leafhoppers near the end of their natural life often become sluggish and inactive, and of all of the dead leafhoppers taken only one dark overwintering adult was found; the remainder were adults of the summer generation.

In the canyons and mountain passes of the northern San Joaquin Valley there are limiting factors which check the multiplication of the

TABLE 3

AVERAGE ANNUAL RAINFALL FROM NORTH TO SOUTH IN SACRAMENTO AND SAN JOAQUIN VALLEYS

Western half		Eastern half	
Station	Rainfall, in inches	Station	Rainfall, in inches
Sacramento Valley			
Red Bluff	24.81	Chico	23.60
Corning	21.36	Oroville	27.50
Willows	16.35	Marysville	19.60
Colusa	15.95	Sacramento	17.96
Woodland	17.88		
Vacaville	26.53		
San Joaquin Valley			
Antioch	12.68	Milton	21.31
Tracy	10.58	La Grange	16.91
Westley	10.65	Lemon Cove	15.14
Newman	11.17	Porterville	10.02
Los Banos	8.10		
Dos Palos	8.29		
Mendota (near valley trough)	5.88		
Coalinga	7.24		
Dudley	7.07		
Lost Hills	5.72		
Middlewater	6.40		
Maricopa	6.36		

leafhopper. Porterville, with an annual rainfall of 10.02 inches, is near the northern limit of the natural breeding area in the Sierra Nevada foothills, on which a low population of insects occurs. Coalinga, situated among the foothills on the western side of the valley, has an annual rainfall of 7.24 inches, and conditions are favorable for the multiplication of the leafhopper. Bakersfield, located in the plains district of Kern County, has an annual rainfall of 5.68 inches, and most of this county is favorable for the insect.

It has frequently been observed that when red-stem filaree grows tall and dense the leafhoppers leave the vegetation. They prefer short filaree on barren hillsides.

The character of red-stem filaree may be an indicator of favorable foothill breeding grounds, but, nevertheless, there may be composite controlling factors which hold this insect in check in some of the canyons and mountain passes of the northern San Joaquin Valley, even where short red-stem filaree occurs. The character of the day from sunrise to sunset is different in the northern part of the San Joaquin Valley from that in the middle and southern sections of the valley—there are more cloudy and partly cloudy days. The northern section of the valley has a lower percentage of sunshine than the middle and southern portions. Fogs moving through Carquinez Strait and spreading over the northern San Joaquin Valley may be another factor in the complex climatic barrier that destroys the overwintering adults.

Exposure and shading of hills is an important factor in the habitat of the overwintering insects. The leafhoppers prefer the south exposure on the hillside when food conditions are favorable, but when the pasture vegetation becomes dry they are sometimes found abundantly on the north slopes.

The leafhoppers prefer gravelly or rocky slopes to soil which holds the moisture. During the spring the nymphs are often seen basking in the sunshine on the warm stones. Frequently the insects are abundant on squirrel mounds.

A critical factor in the reduction of the spring population in the northern San Joaquin Valley may be associated with the hatching of the nymphs. At Manteca eggs deposited in the foliage of sugar beets from November 1 to January 15, 1919, failed to hatch out of doors. It was commonly observed in the greenhouse that eggs will push out of the slit-like egg chamber, but the nymphs often failed to rupture the chorion or died in the process of extrication from the eggs, and this may be associated with humidity and temperature.

In Sacramento Valley.—Rainfall is an important exterminating factor of the beet leafhopper in the Sacramento Valley. The rainfall increases northward in the Sacramento Valley and varies from 17.96 inches at Sacramento near the southern boundary of the valley to 24.81 inches at Red Bluff in the northern extremity. The precipitation is considerably less upon the western side of the valley than in corresponding localities upon the eastern side. The rainfall along the western side decreases from the south to about the central part of the valley and then increases to Red Bluff. The rainfall along the eastern side increases from south to north throughout the valley. Table 3 shows the average rainfall from north to south at the weather bureau stations situated in the western and eastern halves of the valley.

The winter humidity is high owing to rains and fogs in the Sacramento Valley. A low atmospheric humidity accompanied by cloudless skies is usual throughout the summer, and is favorable for the spring migrants and summer progeny of the leafhopper. In the southern portion of the valley the relative humidity is about 10 per cent higher than in the northern part.

Fog is common during the winter months, but decreases in density and frequency of occurrence northward in the Sacramento Valley. In the southern part of the valley, fog is dense during the night and morning, but frequently disappears or lifts during the day, though sometimes it continues as a high fog for several days. The lower-lying parts of the valley are sometimes subject to light fogs in the autumn and spring, when other portions are free from it.

After the serious outbreak of the leafhopper during 1925, adults were found during the autumn in canyons of the Coast Range and in the cultivated areas. Food for the insects had been favorable in the canyons since the October rains had germinated the seeds of red-stem filaree. In the cultivated areas adults were taken during the autumn on spearscale (*Atriplex patula*) (fig. 21) growing along irrigation ditches. During the winter, however, the adults were exterminated in both the canyons and cultivated areas. The exterminating factor was the dense ground fogs which occurred daily from December 22 to January 18. During 28 days of this fog period there were only 4 hours of sunshine. Rainfall apparently was not the direct exterminating factor during the fog period. The precipitation during the 28 days of fog at Sacramento was as follows: January 2, 0.02; 14, 0.03; 16, 0.01; 18, 0.15; total, 0.21 inches.

Another factor unfavorable to the overwintering adults may be the heavy dew which occurs during the rainy period in the Sacramento Valley.

The Sacramento Valley has a lower percentage of sunshine than the middle and southern parts of the San Joaquin Valley.

In the cultivated areas of the Sacramento Valley the most favorable breeding plants, such as the saltbushes, are scarce, except in the southern part of the valley. But red-stem filaree is abundant on the foothills of the Coast Range and on the west side of the Marysville Buttes, and hence food and breeding plants are not the limiting factors which prevent the leafhopper from establishing itself in the Sacramento Valley.

After the beets were harvested in the Sacramento Valley during the 1925 outbreak of the beet leafhopper, large numbers of leafhoppers flew into adjacent bean fields, and a high mortality of the insects occurred.

Dead leafhoppers with their mouth parts inserted in the tissues of the leaves were common on pink beans. In all probability a high mortality of the nymphs occurs after the beets are harvested and the tops become dry, although large numbers of leafhoppers were found on

Fig. 21. Branch of spearscale (*Atriplex patula*) showing leaves and fruiting bracts, also different-shaped leaves removed from plant.

Atriplex patula growing along irrigation ditches after the beets were harvested.

When insects migrate from their natural breeding grounds, they fail to establish themselves in their new environment unless they encounter conditions similar to their original habitat. When the migrating swarms of the beet leafhoppers invade the beet fields under new conditions of environment, barriers rarely affect the migrants, which usually destroy the beet crop when they are at their maximum in numbers. The hot, dry summers in the Sacramento Valley are favorable to the migrants and later generations in the cultivated areas, but the overwintering progeny is exterminated by the winter conditions.

In Salinas Valley.—Rainfall above normal is a factor which reduces the beet leafhopper in its natural breeding areas in the Salinas Valley. There is not only a wide variation in the rainfall of the Salinas Valley from year to year, but often considerable variation for the same season in different parts of the valley. The rainfall diminishes as the head end of the valley is approached, although this is subject to variation, and the seasonal rainfall at Soledad averages less than at either Salinas or King City. The seasonal rainfall may vary from 5 inches or less in one season to over 20 in the following. Salinas, in the northern portion of the valley, has an annual rainfall of 13.96 inches; Soledad, in the central part, 8.95 inches; and King City, in the southern portion, 11.32 inches.

The variation in rainfall from year to year in the Salinas Valley has a marked effect on the overwintering adults on the foothills. During successive heavy rainy seasons the spring population of leafhoppers which invaded the cultivated areas was often reduced to a minimum, and average or high yields of beets were often obtained. The seasonal rainfall during 1914–15 was 15.72 inches at the Spreckels ranch near King City and no leafhoppers or curly top were reported to have occurred in the beet fields. During 1909 an average of 15.37 tons per acre were harvested on the Spreckels ranch near King City and the seasonal rainfall was 15.64 inches. On the other hand, during 1907 an average of only 8.6 tons per acre were harvested, yet the seasonal rainfall was 19.98 inches; 12.00 and 13.75 inches had occurred during the two previous rainy seasons.

According to the Weather Bureau of the United States Department of Agriculture the seasonal rainfall at King City was as follows: 1914–15, 11.50; 1908–09, 13.51; 1906–07, 20.54; 1905–06, 12.91; 1904–05, 14.33 inches.

The seasonal rainfall at King City during severe outbreaks of the beet leafhopper is shown in table 4.

TABLE 4

SEASONAL RAINFALL IN THE KING CITY DISTRICTS DURING OUTBREAKS OF BEET LEAFHOPPER

Year	Spreckels ranch near King City	U. S. Department of Agriculture Weather Bureau, King City
	inches	*inches*
1898–99	7.07	7.07
1899–1900	8.60	7.42
1900-1901	16.40	16.22
1904 05	13.75	14.33
1913–14	15.64	14.61
1918–19	11.09	8.78
1921–22	13.15	12.12
1924–25	5.86	6.25
1926–27	10.29	9.79

During 1899, 1900, and 1901 irrigation facilities when needed were inadequate, but the failure of the sugar-beet crop could largely be attributed to curly top. During 1919, 55 per cent of the sugar beets were infected with curly top before the spring flights occurred from the foothills (fig. 22) by the overwintering adults which had remained in the cultivated areas. The migrations of the leafhoppers from the San Joa-

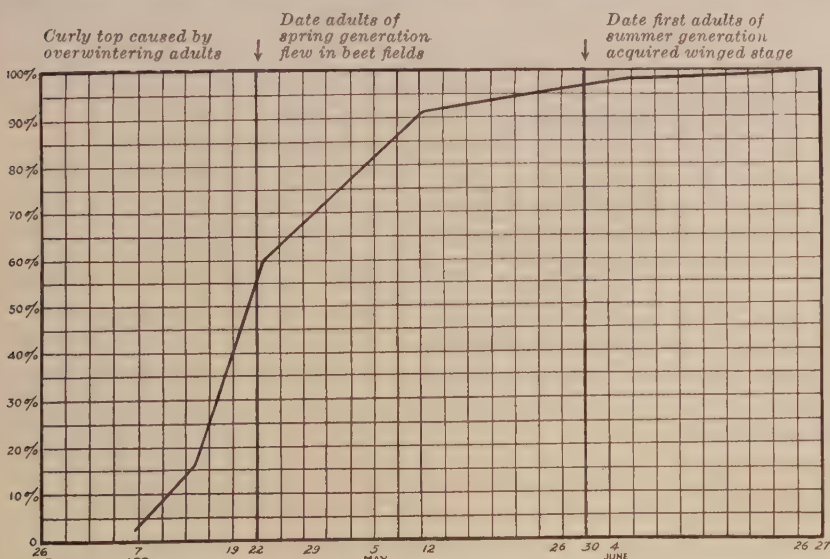

Fig. 22. Chart showing that 55 per cent of the beets in the Salinas Valley were infected with curly top by the dark overwintering adults which occurred in the cultivated areas of the Salinas Valley before the first adults of the spring generation flew into the beet fields. (Adapted from a chart by W. W. Thomas, formerly employed by the Spreckels Sugar Company.)

quin into the Salinas Valley during 1922, 1925, and 1927 have already been discussed. During 1901, 1905, and 1914 the rainfall was sufficient to reduce the population of leafhoppers on the Salinas foothills, and the severe outbreaks of the leafhoppers must have been due to migration from the San Joaquin Valley.

A comparison of the seasonal rainfall from north to south in the San Joaquin Valley with King City in the Salinas Valley is made in table 5.

TABLE 5

COMPARISON OF RAINFALL FROM NORTH TO SOUTH IN SAN JOAQUIN VALLEY WITH KING CITY, SALINAS VALLEY

Station	1900–01	1904–05	1913–14	1921–22	1924–25	1926–27	Average annual rainfall
Tracy	14.10	15.05	12.17	....	....	10.51	....
Westley	13.71	11.65	17.08	7.98	....	....	....
Newman	12.08	14.42	16.20	....	9.46	10.55	....
Los Banos	11.37	11.83	....	....	....	8.20	....
Firebaugh	....	....	9.70	10.38	7.70	6.40	....
Mendota	10.89	9.53	....	....	....	....	....
Coalinga	....	....	9.65	9.62	4.64	8.34	7.24
Dudley	....	....	8.14	8.14	5.36	7.67	7.07
Antelope Valley	....	....	10.61	11.51	4.62	....	....
Bakersfield	....	8.27	7.35	8.88	4.69	6.20	5.68
Maricopa	....	....	9.97	8.75	3.52	7.30	6.36
King City*	16.40	13.75	15.64	13.15	5.86	10.29	....
King City†	16.22	14.33	14.61	12.12	6.25	9.79	11.32

* Spreckels ranch near King City.
† U. S. Department of Agriculture Weather Bureau, King City.

It is evident from table 5 that during the 1900, 1905, and 1914 outbreaks of the pest the seasonal rainfall was unfavorable in the northern San Joaquin Valley but favorable in the middle and southern parts of the valley.

Dessicating winds in the Salinas Valley may be an important indirect controlling factor affecting the water balance of the leafhopper, especially when it feeds on weeds which wilt and become sunscorched during hot days. During extremely hot spells the leafhoppers will leave wilted, sunscorched weeds and seek other food plants; but the change to certain food plants results in a mortality of the nymphs and adults.

In Coastal Regions.—Fog is the most important barrier when the beet leafhoppers migrate into the coastal regions. During the 1925 outbreak, the insects migrated across San Pablo Bay into the beet fields along the coast near Ignacio. The April plantings showed an average of 60 per cent curly top on July 15, while in the June plantings no curly

top or beet leafhoppers were found. A single nymph was found in the April plantings during a half day's search. An examination of the same fields on August 1 showed that all of the beets in the April plantings were diseased, while in the June plantings 16 per cent of the beets adjacent to the April plantings, were diseased and an average of 10 per cent of the beets in isolated June plantings showed curly-top symptoms. No fungus-diseased leafhoppers were found. Most of the offspring of the spring migrants were probably exterminated by fogs, possibly augmented by low temperatures associated with them.

In determining the life history of the leafhopper in the fog belt at Berkeley, 22 adults of the first generation were reared between May 15 and June 23. A single adult of the second generation was bred from eggs deposited by the 22 adults on October 21.[30] The egg-laying capacity of a single female kept out of doors at Manteca situated in the northern San Joaquin Valley was 328 eggs.[35] Fogs and probably low temperatures were the limiting factors which prevented a large population from developing in cages out-of-doors.

FLUCTUATIONS IN POPULATION

Early Drying of Pasture Vegetation.—The factors associated with the reduction in numbers of the spring generation vary in different years. In some years dessicating northerly winds dried the pasture vegetation rapidly during the spring and hence large numbers of eggs failed to hatch. In all probability when red-stem filaree becomes wilted many eggs fail to hatch, as is the case when sugar-beet leaves and weeds wilt in the greenhouse.

The primary cause for the enormous reduction in numbers of the beet leafhoppers on the uncultivated plains and foothills during 1923 was the early drying of the pasture vegetation. Drought conditions from the middle of February to the close of March dried the filaree in March instead of in April and May as in a normal season. In some years the pasture vegetation dried so rapidly in the southern section of the San Joaquin Valley that many nymphs failed to acquire the winged stage. During the spring of 1931, however, when a low population of leafhoppers occurred in Little and Big Panoche passes owing to the rapid drying of the pasture vegetation during early April, a high population was present in the southern San Joaquin, where more rainfall kept the pasture vegetation green.

Destruction of Pasture Vegetation by Aphids.—During the spring of 1927 aphids were extremely abundant in the middle San Joaquin and

destroyed most of the red-stem filaree during March, and thus reduced the food supply before many of the leafhopper nymphs acquired the winged stage. According to Schwing, 90 per cent of the red-stem filaree was destroyed on the foothills in the vicinity of Coalinga. In Little and Big Panoche passes most of the red-stem filaree was also destroyed by aphids.

Early Autumn Rains.—One factor favorable for the increase of the beet leafhopper during the 1919 outbreak of the pest was the heavy rainfall on September 11 to 13, 1918, germinating the seeds of the pasture vegetation on the uncultivated plains and foothills, and resulting in a new growth of weeds in the cultivated areas of the San Joaquin and Salinas valleys. During the autumn the saltbushes and other favorable host plants of the leafhopper normally become dry. In 1918, however, the nymphs which hatched from eggs deposited in the fall by the females of the summer generation found an abundance of food in this new growth of vegetation in the cultivated districts. Many of these nymphs acquired the winged stage after the return flights of the overwintering adults to the plains and foothills during October and November.

Nymphs were also taken during November and December, 1918, on red-stem filaree growing on the foothills of the San Joaquin and Salinas valleys. These nymphs hatched from eggs deposited in filaree by the females of the summer generation and not by the overwintering forms.

Late Spring Rains.—A partial second brood develops on the uncultivated plains and foothills of the San Joaquin Valley whenever late spring rains occur and the pasture vegetation remains green. As already stated, a partial second brood developed on the foothills of the Salinas Valley during the 1925 outbreak of the pest.

Spring and Summer Migrations.—Spring migrations reduce the number of beet leafhoppers, since no return flights to the natural breeding areas occur.

Summer migrations may deplete the natural breeding grounds of the beet leafhopper to a large extent; the nymphs and adults are then hard pressed by parasites and predaceous enemies. The observations on the summer migrations from the San Joaquin Valley during 1919 have been given in this paper.

NATURAL ENEMIES

PREDATORS

According to Hartung[17] three predaceous bugs prey on the beet leafhopper in California: *Neides muticus* Say; *Zelus socius* Uhl; and *Reduvicolis kalmi* Reut.

Specimens of *Geocoris pallens* Stål were frequently seen in the field sucking out the juices of nymphs and adults. A reddish mite attached to the body of the beet leafhopper was sometimes observed (plate 4, *B*).

During 1925 the green lacewing (*Chrysopa californica* Coq.) (fig. 23) was extremely abundant in the beet fields about 5 miles west of Terminus in the San Joaquin Valley. The eggs (fig. 23 *B*) were found on the blades and petioles of every beet examined. The green-lacewing larva devoured the nymphs and adult leafhoppers in cages.

Spiders were noticed feeding on the leafhoppers on the uncultivated plains and foothills and in the cultivated areas.

In the greenhouse control measures must be adopted against the Argentine ant (*Iridomyrmex humilis* Mayr), which enter the cages, kill the nymphs, and occasionally the adults, and carry them to their nests.

PARASITES

Hartung[17] bred three egg parasites from the eggs of the beet leafhopper; these were determined by A. A. Girault to be *Abbella subflava* Gir.; *Anaphes* sp. near *hercules;* and *Gonatocerus* sp. The last two egg parasites emerged from eggs of the leafhopper from Ravendale, Lassen County, California.

Stahl[41] bred *Abbella subflava* Gir. from the eggs of the beet leafhopper at Riverside and called attention to the fact that this is a primary parasite and not a hyperparasite as Hartung[17] states. Stahl reared two egg parasites, *Polynema eutettigis* Gir. and *Anagrus giraulti* Craw., at Spreckels and Riverside.

Severin[31] bred four egg parasites from the eggs of the beet leafhopper in the San Joaquin Valley: *Polynema eutettigis* Gir. (plate 5, *A, B*); *Anagrus giraulti* Craw. (plate 5, *C, D*); *Apelinoidea plutella* Gir.; and *Anthemiella rex* Gir. These egg parasites were reared more abundantly from eggs deposited by the leafhopper in saltbushes than in sugar beets.

The writer, in cooperation with C. F. Henderson, bred a single specimen of *Ufens* n. sp., presumably from eggs of the beet leafhopper de-

posited in red-stem filaree growing in the Little and Big Panoche passes during the spring of 1928. *Aphelioidea plutella* Gir. has been bred from eggs deposited in red-stem filaree collected in the vicinity of Coalinga,

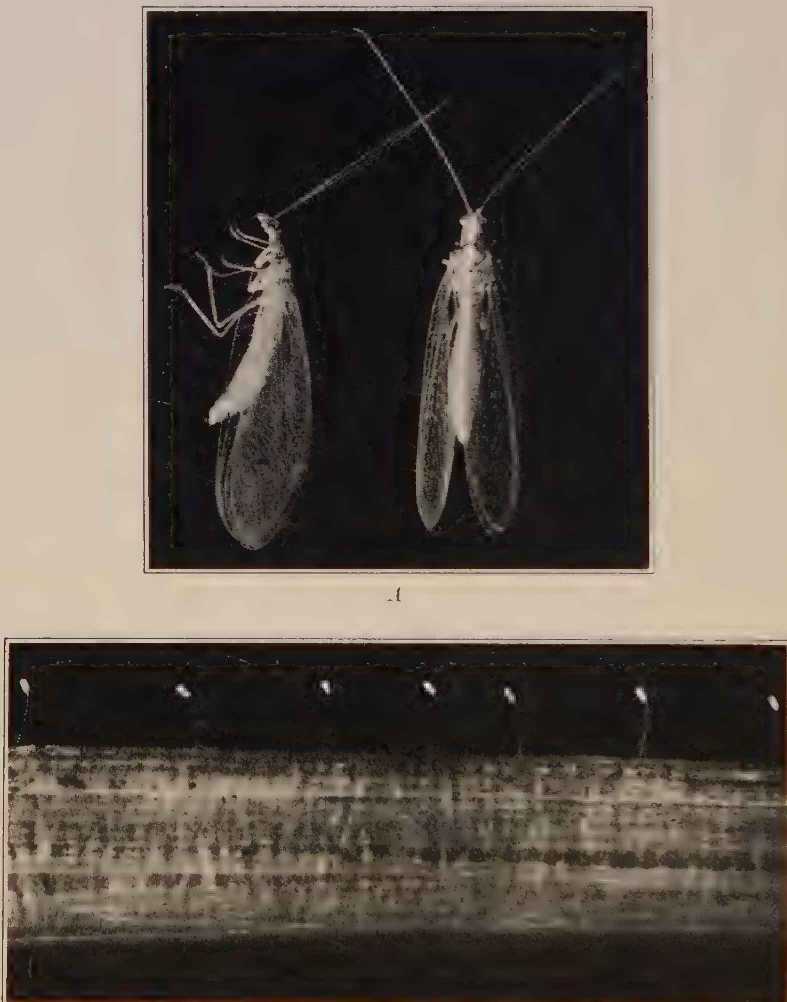

Fig. 23. Green lacewing (*Chrysopa californica* Coq.): *A*, adults; *B*, eggs deposited on the petiole of a sugar-beet leaf.

but no egg parasites other than these two have been reared from material collected on the plains and foothills up to the present time.

Two parasitic flies were bred from the beet leafhopper: *Pipunculus vagabundus* Knab (plate 6, *A, B*) and *P. industrius* Knab. The *Pipun-*

culus flies deposit an egg in the nymph or adult leafhopper. The egg hatches into a larva or maggot which feeds within the abdomen of the leafhopper (plate 6, *D*). When the larva is full grown (plate 6, *E*) it bores out of the host, leaving an exit hole (plate 6, *F*), usually near the junction of the metathorax and abdomen. The leafhopper is killed after the larva emerges. After escaping from its host, the larva buries itself beneath the soil and pupates (plate 6, *G*). At Spreckels the flies issued after remaining in the pupal stage (plate 6, *H*) for a period of 22 days during the summer.[19]

A wingless female ant-like wasp, *Gonatopus contortulus* Patton (plate 4, *A;* plate 7, *B*), and the winged male (plate 7, *A*) were bred from the beet leafhopper. The ant-like female is a very active creature, capturing and partly devouring a large number of leafhoppers. A single parasite emerging in a cage will kill most of the leafhoppers, but only in an occasional host is an egg deposited. The presence of the parasite in its later development can be determined by the external brown sac in the nymph or beneath one of the wings in the adult leafhopper (plate 7, *C*). After the full-grown larva bores out of the leafhoppers (plate 7, *D, E*) it leaves in the exit hole the larval sac consisting of the molted skins of the larva (plate 7, *F*). The larva spins a white cocoon (plate 7, *H*) 3 mm long and 1 mm wide, on the foliage of the saltbush or beet leaf. Forty days after spinning its cocoon the wingless parasite emerged on October 24, 1914, at Spreckels.[19]

In 1913 about 3.2 per cent and in 1914 about 33.6 per cent of the beet leafhoppers collected in the beet fields were found to be parasitized by *Pipunculus vagabundus, P. industrius,* and *Gonatopus contortulus.*[19]

During 1918–1920 a comparison was made of the percentage of parasitized beet leafhoppers collected on the uncultivated plains and foothills with those captured in the cultivated areas of the San Joaquin Valley. Records obtained by dissecting the adult were more reliable than those secured by breeding the parasites, since a high mortality of the insects occurred in the breeding jars. The average percentage of parasitized adults of various generations by *Pipunculus* and *Gonatopus* is indicated in table 6.

According to table 6, in 1919 the percentage of parasitism gradually increased during the summer months in the cultivated areas and reached its height during August. The weak point in the parasitism occurs on the uncultivated plains and foothills. Table 6 shows that 4.4 per cent of the overwintering adults collected on the plains and foothills were parasitized compared with 28.0 per cent of the overwintering adults captured in the cultivated areas. Dissections show that leafhoppers of the

autumn generation parasitized by a large larva remain in the cultivated areas, although leafhoppers parasitized by a tiny larva fly to the foothills.

A parasitic hairworm (plate 4, *C*, *D*) belonging to the Gordiaceae emerged and was also dissected on rare occasions from the beet leafhopper. A case of double parasitism by a hairworm and a *Pipunculus* larva occurred in the abdomen of an overwintering female collected on the foothills near King City in the Salinas Valley on November 28, 1918.

TABLE 6

Parasitism of Beet Leafhopper on Plains and Foothills and in Cultivated Areas of San Joaquin Valley

Uncultivated plains and foothills				Cultivated areas			
Year	Months	Generation	Average percentage parasitism	Year	Months	Generation	Average percentage parasitism
1918–19	Nov.-Mar.	winter	8.2	1918	Dec.	winter	28.0
1919	Apr.	spring	1.0	1919	Apr.-May	spring	3.5
1919–20	Oct.-Feb.	winter	4.4		June	summer	10.0
1920	Apr.	spring	1.5		July	summer	22.3
					Aug.	summer	35.1
					Sept.	summer	32.0
					Average, June-Sept.	summer	24 8

The beet leafhopper is also parasitized by an occasional *Stylops*, which was not bred.

Since it had been reported by Bonequet[4] that the beet leafhopper, as well as curly top of sugar beets, occurred in Argentina, an exploration for parasites of this insect was undertaken in that country by the University of California in cooperation with the United States Department of Agriculture, Bureau of Entomology.

According to Bonequet[4] the beet leafhopper has been found in the vicinity of "Buenos Aires, in Guatrache, Alpachiri, and Bahia Blanca (southeast), in Colonia Alvear and Mendoza (west) covering the major part of the temperate and subtropical zones of the Argentine Republic." Leafhoppers which were reported to have been collected at San Isidro, a suburb of Buenos Aires, were determined as *Eutettix tenellus* (Baker) by E. P. Van Duzee and the writer, and are in the collections of the California Academy of Sciences.

Henderson, who was sent to Argentina to introduce parasites of the beet leafhopper into the United States, swept the most favorable host plants of the beet leafhopper with an insect net in the localities reported

by Boncquet, and many other localities, from November 11, 1926, to June 30, 1927, but failed to find *Eutettix tenellus.* Insect collections in museums and of entomologists were examined, but not a single specimen of *E. tenellus* was found. An undetermined species of *Eutettix* resembling the general shape and size of *E. tenellus* was collected by Henderson on sugar beets, garden or red beets, and Swiss chard in every locality in which Boncquet reported that *E. tenellus* occurred except in Guatrache.[36] Henderson[20] has published a detailed report on the exploration in Argentina for the beet leafhopper.

Fawcett[13, 14] demonstrated that a disease of sugar beets in Argentina resembling the foliage symptoms of curly top in North America, was transmitted by *Agallia sticticollis* Stål.

Since the beet leafhopper was known to occur in the western part of North America from Canada into Mexico, an exploration of Mexico for parasites of the leafhopper was undertaken, for it was thought that possibly the original native home of the insect was Mexico, and that the insect through migratory flights had established itself in localities outside the range of its efficient parasites.

Henderson[7] explored Lower California, the west coast and the central district of Mexico, Arizona, Utah, and southern Idaho for parasites of the beet leafhopper during the period from October 3, 1927, to July 16, 1928. He states: "Neither the beet leafhopper nor parasites were found on the high central plateau, which extends from the southern portion of Durango to Mexico City. For the west coast, although the territory from Nogales, Arizona, to Mazatlan, Sinaloa, was covered, the range of the leafhopper apparently extended only as far south as Guasave, Sinaloa." Egg parasites occurred over the entire area occupied by the insect, most of which had previously been bred by other workers from the eggs of the beet leafhopper in California.

Fungus Disease

Fungus diseases kill some of the overwintering leafhoppers and spring migrants (plate 8), as reported in previous papers.[28, 31] During December, 1918, large numbers of leafhoppers were collected on the foothills bounding a canyon in the northern San Joaquin Valley 13 miles southwest of Tracy. When these insects were confined in cages in the greenhouse at Berkeley, they died as a result of a fungus disease. The weather records kept by the Spreckels Sugar Company at Manteca showed that the precipitation from September to April was 17.29 inches; 9.98 inches of rain fell from September to December. During the

1919 outbreak of the pest, the spring migrants succumbed to a fungus disease in the fog belt of San Luis Obispo and Santa Barbara counties. An examination of the lower surface of the leaves of a single sugar beet showed 178 jassids, including beet leafhoppers, which had died as a result of a fungus disease. In regions outside of the fog belt, however, no dead fungus-diseased insects were found that year, and near Los Alomos, nymphs and adults were abundant in the beet fields.

SUMMARY

The northern limit of the breeding range of the beet leafhopper in the San Joaquin Valley was found to be in a canyon in the Mount Diablo Mountains situated about 4 miles southwest of Pittsburg. The natural breeding area includes the canyons of the Mount Diablo Range in northern section, the plains and foothills of the Inner Coast Range in the middle and southern sections, and the foothills of the Tehachapi Mountains in the southern section of the San Joaquin Valley. The plains and foothills of most of Kern County are natural breeding grounds, except the Sierra Nevada foothills near the northern end of the county. The northern limit of the breeding range on the Sierra Nevada foothills was found to be about 10 miles north of Porterville near Lindsay in Round Valley.

A natural breeding area occurs between the Coast Ranges on the western foothills of the Panoche Hills bounding Panoche Valley.

The northern limit of the foothill breeding range on the Gabilan Mountains in the Salinas Valley is at the boundary of the fog belt south of Soledad and the southern limit in the vicinity of San Miguel, the most favorable foothill breeding area being from Greenfield to Bradley.

A natural breeding area extends from Santa Ana Valley to Panoche Pass, becoming less favorable toward Pacheco Pass.

A natural breeding grounds occurs in Honey Lake Valley at an altitude of about 4,000 feet in the Sierra Nevada. The beet leafhopper was also found in the Sierra Valley and was reported to occur in the American and Indian valleys.

The beet leafhopper was taken on twenty species of food plants growing on the uncultivated plains and foothills, five of which belong to the Chenopodiaceae, to which the sugar beet belongs. The nymphs were bred from eggs deposited in eight different species of plants under natural conditions. Red-stem filaree is the most important host plant upon which the overwintering adults feed and deposit their eggs, and upon which the spring generation develops.

When the beet leafhopper is abundant it occurs on most weeds and a large number of economic plants. Nymphs have been bred from eggs deposited in forty-six different annual and perennial plants growing in the cultivated areas; nineteen of these breeding plants belong to the Chenopodiaceae and the remainder to twelve other families.

The range of the beet leafhopper corresponds to the geographical distribution of the saltbushes. Further breeding experiments are necessary to determine whether the native mustards were the original host plants of the leafhopper.

The spring dispersal of the leafhopper from the uncultivated plains and foothills occurs after the pasture vegetation becomes dry and is probably associated with a food stimulus, the insects invading the cultivated areas when the annual saltbushes and other weeds are succulent and most favorable from the standpoint of food and egg deposition.

The spring flights have frequently been observed from the entrance of Little Panoche Pass and appear to be associated with air currents at sunset. The ascending air currents may carry the insects into the higher winds and here they may drift and fly long distances, possibly over mountain ranges. When the pest was at the maximum in numbers immense swarms flew into the cultivated areas. One swarm from the plains and foothills of the middle San Joaquin flew across the valley, a distance of about 50 miles. A succession of northward flights occur in the cultivated areas of the San Joaquin Valley and apparently the insects fly against light northwest winds.

A spring migration of the leafhopper occurs from the cultivated areas of the San Joaquin into the Sacramento Valley. Flights of small numbers of leafhoppers precede the large migration into the Sacramento Valley. Spring migrations from the San Joaquin Valley have occurred across Suisun and San Pablo bays, into Livermore Valley, San Francisco Bay districts, Santa Clara, San Juan and Salinas valleys, and possibly into the fog belt of the southern counties. The distance of a migratory flight from the San Joaquin into the Sacramento Valley was estimated at about 60 miles, and successive northward migrations following the cultivated areas of the Sacramento Valley at about 150 miles.

The dispersal of the summer generation from badly diseased beets to healthy beets is known to extend at least 3 miles in the Sacramento Valley.

Summer migrations of the beet leafhopper from the San Joaquin Valley occurred during the 1919 outbreak of the pest. These migrations were probably associated with overcrowding and unfavorable food.

The autumn dispersal from the cultivated areas to the uncultivated plains and foothills in the San Joaquin and Salinas valleys occurs during October, November, and December. During the autumn dissemination the insects congregate on favorable weeds growing on abandoned farms on or near the plains. Frequently the lines of flight across the plains to the canyons and mountain passes follow dry creek beds where the insects take short flights from perennial to perennial. The leafhoppers also occur on perennials growing on the plains. The autumn flights of the leafhopper are probably associated with a food stimulus; the insects fly from the cultivated districts when the saltbushes and other favorable weeds become woody and dry.

The most important natural barrier of the beet leafhopper is rainfall. which reduces the population on the northern foothills of the San Joaquin Valley. The abundance of rainfall in the Sacramento Valley is the factor that exterminates the overwintering adults on the foothills and in the cultivated areas. Rainfall when above normal reduces the population on the foothills in the Salinas Valley. Fog and possibly low temperatures are limiting factors to the offspring of the migrants when the leafhopper migrates into the coastal regions. Various composite controlling factors, such as high humidity owing to rains and fogs, heavy dew, soil moisture, tall dense filaree, cloudiness or low temperatures, may play important roles in the survival of the insect during the hatching and molting process. The succession of favorable food plants throughout the season may also be a limiting factor in certain migratory areas of the insect, such as the middle and northern Sacramento Valley.

The factors associated with the reduction in numbers of the spring generation vary in different years. In some years dessicating northerly winds dry the pasture vegetation rapidly during the spring and hence large numbers of eggs fail to hatch. The primary cause for the enormous reduction in numbers of the spring generation during 1923 was the early drying of the pasture vegetation during March instead of April and May, so that many nymphs died before they acquired the winged stage. During the spring of 1927 aphids destroyed most of the filaree in the middle San Joaquin Valley, reducing the spring population of beet leafhoppers.

The primary cause for the enormous increase of the beet leafhoppers during 1919 hinges on two factors: (1) There were no summer migrations of the pest from the natural breeding grounds during 1918, so that large numbers of eggs were deposited during the autumn; (2) the nymphs which hatched from these eggs found an abundance of green food, not only in the cultivated areas but also on the uncultivated plains

and foothills, after the heavy September rains germinated the seeds of the vegetation.

Another factor favorable for the increase of the beet leafhopper on the uncultivated plains and foothills is late spring rains, which keep the pasture vegetation green so that a partial second brood develops.

Among the natural enemies of the beet leafhopper are a large number of predacious insects which prey upon the nymphs and adults. Seven species of egg parasites, two species of *Pipunculus* flies, a *Gonatopus*, and a hairworm were bred by various entomologists in California. In 1919 the percentage of parasitized leafhoppers gradually increased during the summer months and reached its height during August (35.1 per cent). The weak point in the parasitism of the leafhoppers occurred on the uncultivated plains and foothills where only 4.4 to 8.2 per cent were parasitized during the winter and 1.0 to 1.5 per cent during the spring. No information is at hand as to the value of egg parasites on the uncultivated plains and foothills and in the cultivated areas.

Fungus diseases reduce the numbers of overwintering leafhoppers and spring migrants in the fog belt in favorable years.

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PLATES

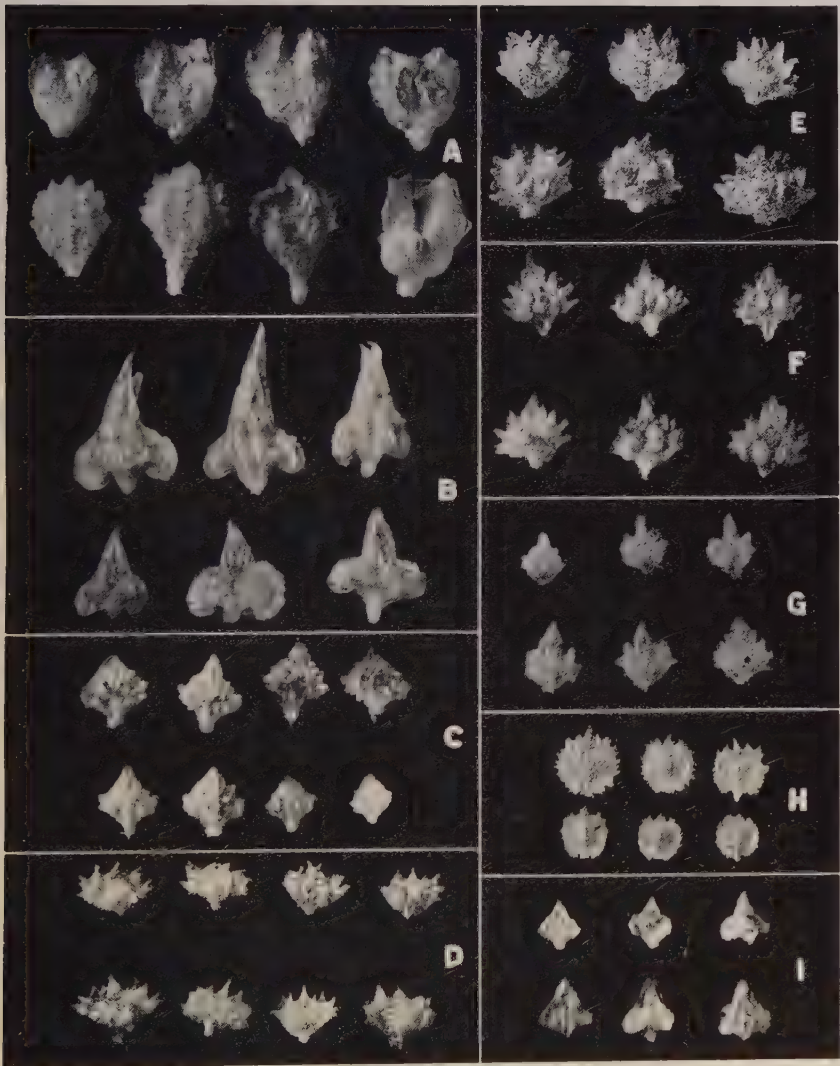

Plate 1. Fruiting bracts of annual saltbushes. These structures have been almost universally considered as modified upper leaves enclosing the seeds. *A*, Fogweed or silverscale (*Atriplex argentea expansa*); *B*, arrowscale (*Atriplex phyllostegia*); *C*, red orache, or redscale (*Atriplex rosea*); *D*, bractscale (*Atriplex bracteosa*); *E*, crownscale (*Atriplex coronata*); *F*, heartscale (*Atriplex cordulata*); *G*, *Atriplex tularensis*; *H*, wheelscale (*Atriplex elegans*); *I*, brittlescale (*Atriplex parishi*).

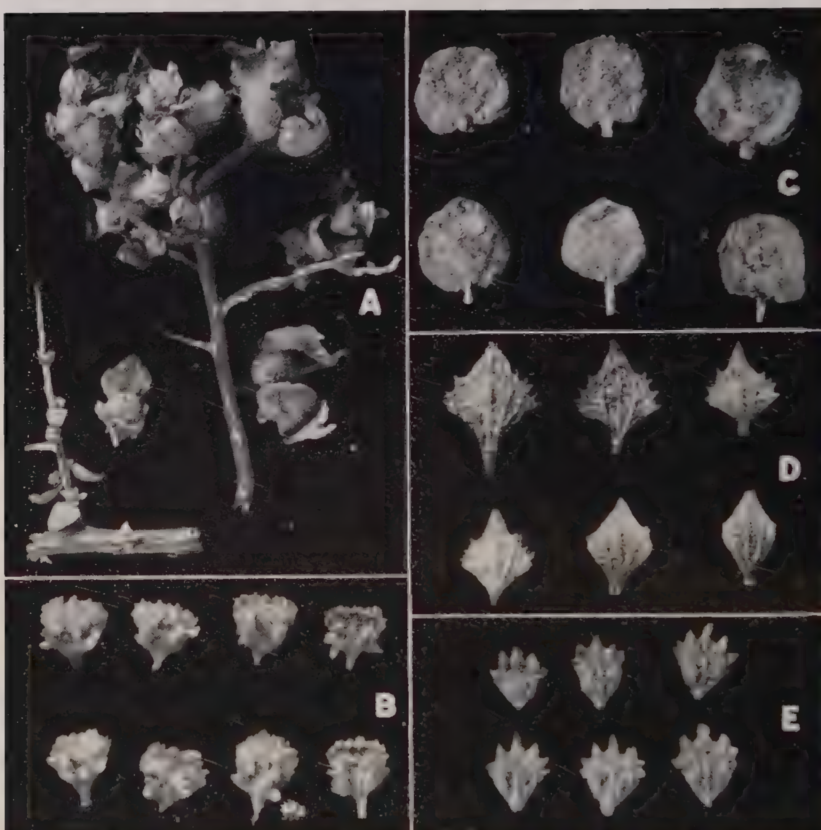

Plate 2. Fruiting bracts of perennial saltbushes: *A*, spinescale (*Atriplex spinifera*), showing clusters of fruiting bracts on spiny branch, also a single fruiting bract showing wings; *B*, cattle spinach or allscale (*Atriplex polycarpa*); *C*, quailbrush or lenscale (*Atriplex lentiformis*), showing compressed rounded fruiting bracts; *D*, fleshscale or Australian saltbush (*Atriplex semibaccata*). Fruiting bracts are convex, fleshy-thickened, and turn red in living plants, but are compressed and nearly flat when dry. *E*, Ballscale (*Atriplex fruiticulosa*).

Plate 3. Branches of four annual saltbushes showing leaves and fruiting bracts, also shape of leaves and fruiting bracts removed from plants: *A*, brittlescale (*Atriplex parishi*); *B*, *Atriplex tularensis*; *C*, heartscale (*Atriplex cordulata*); *D*, bractscale (*Atriplex bracteosa*).

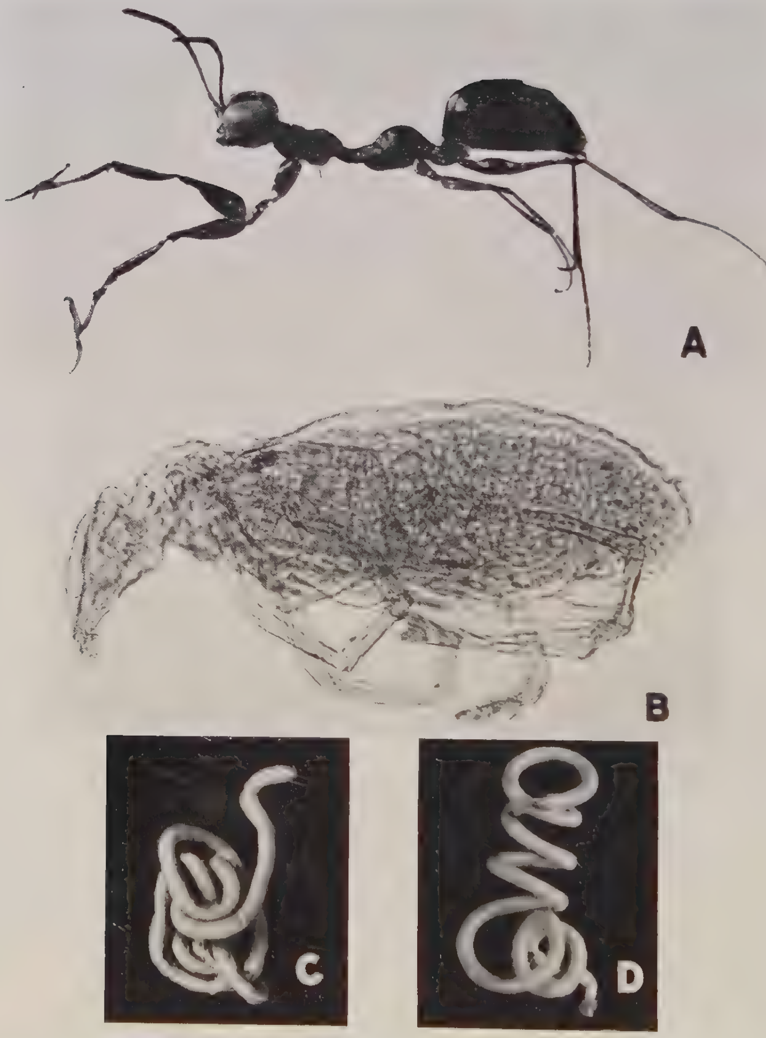

Plate 4. *A*, Female of *Gonatopus contortulus* Patton showing front legs adapted for grasping prey. *B*, Reddish mite removed from leg of a beet leafhopper. *C*, *D*, Parasitic hairworms of beet leafhopper.

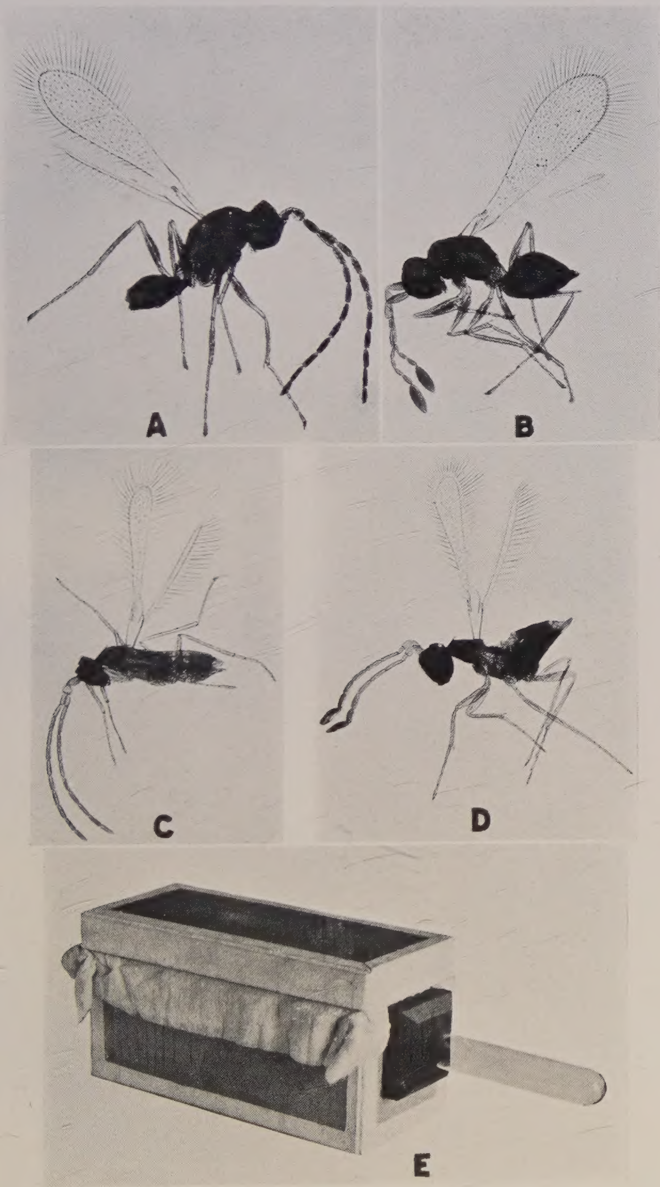

Plate 5. Egg parasites of beet leafhopper and breeding box: *A*, male of *Polynema eutettigis* Gir.; *B*, female of *Polynema eutettigis*; *C*, male of *Anagrus giraulti* Craw.; *D*, female of *Anagrus giraulti*; *E*, egg-parasite breeding box. The egg parasites upon emerging are positive to light and enter the test tube.

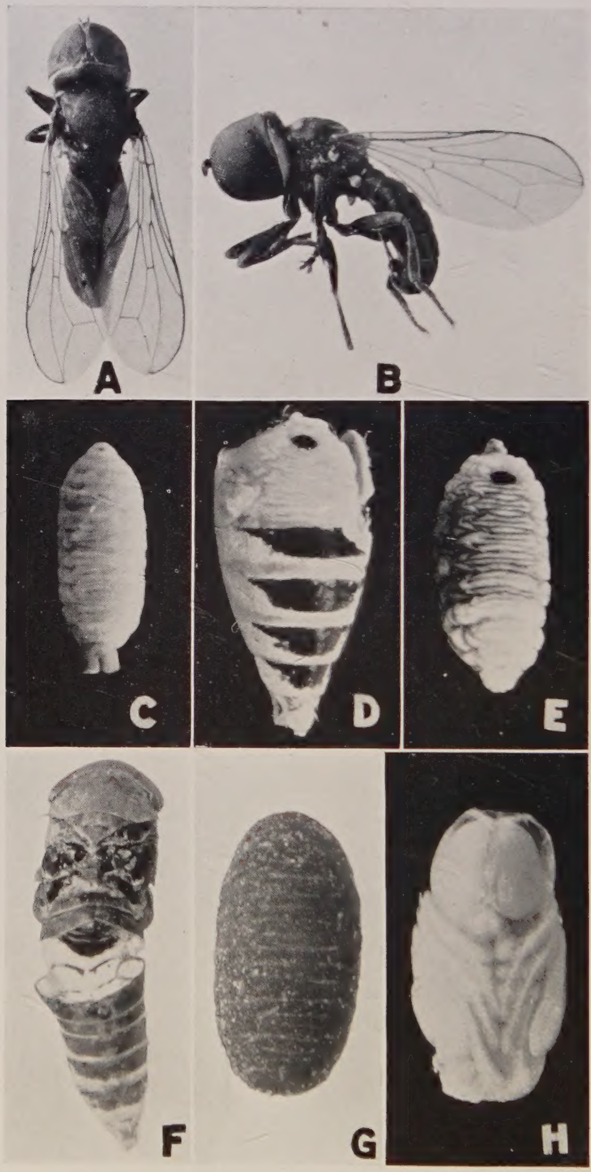

Plate 6. Stages of big-headed fly or *Pipunculus*, a parasite of the nymphs and adults of the beet leafhopper: *A*, male of *Pipunculus vagabundus* Knab.; *B*, female of *Pipunculus vagabundus*; *C*, immature larva showing respiratory tubes; *D*, larva in the abdomen of the beet leafhopper; *E*, full-grown larva after boring out of the beet leafhopper; *F*, beet leafhopper showing large exit hole through which a *Pipunculus* larva bored out; *G*, puparium; *H*, pupa.

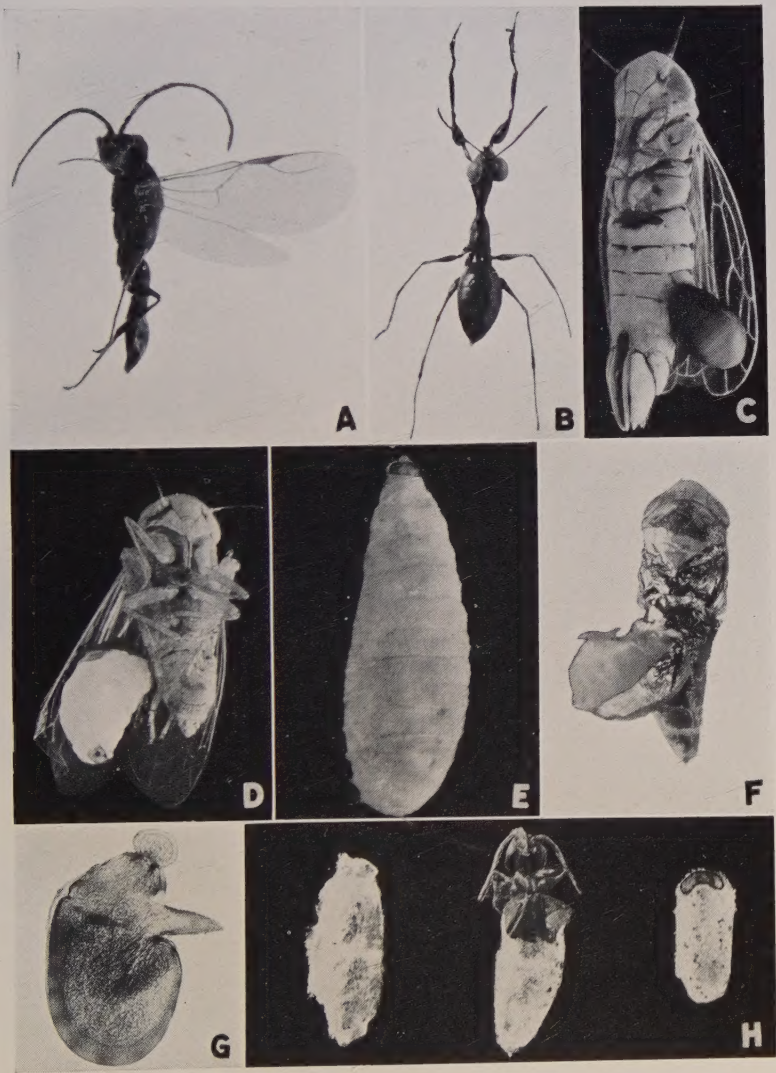

Plate 7. Stages of *Gonatopus contortulus* Patton, a parasite of the nymphs and adults of the beet leafhopper: *A*, male; *B*, female; *C*, dark-brown larval sac beneath the wing of the beet leafhopper; *D*, larva boring out of the beet leafhopper; *E*, full-grown larva after boring out of the beet leafhopper; *F*, larval sac consisting of molted skins of larva; *G*, third instar showing head lobe and ventral larval process; *H*, left, oval white cocoon; center, female that died in cocoon; right, cocoon showing irregular hole which adult gnawed before issuing.

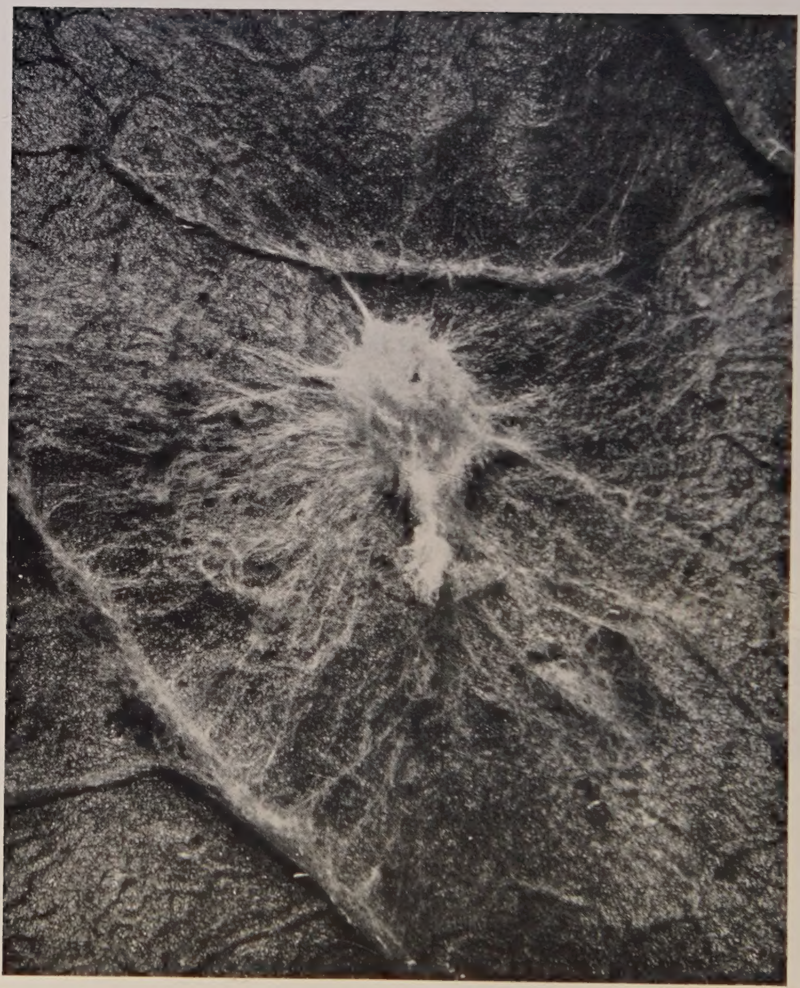

Plate 8. Fungus-diseased beet leafhopper, enlarged, showing mycelium and scattered spores.